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A MONOGRAPH OF THE GENUS PHILADELPHUS

SHIU-YING HU

With six plates

INTRODUCTION

Philadelphus is geographically one of the most widely distributed genera in nature, ecologically one of the most varied groups in habitat, and horticulturally one of the most popular shrubs in our gardens. Its slightly discontinuous distribution forms a belt girdling the temperate zone of the northern hemisphere, extending to the higher altitudes in the tropics in North America. The early inhabitants of Asia Minor, Eastern Asia and Central America, centers where different culture patterns originated, have independently discovered its merits and have brought under cultivation many species for their showy flowers, their enticing fragrance, or for their medicinal value. In ancient times the Parthians employed the flowers in the preparation of hair perfume, and the advanced people of Mexico, and apparently those of Central America, used the flowers for making garlands, and the leaves for medicine. By the early part of the eleventh century, the Chinese garden forms had developed to such a degree of excellence that they were presented by the people of Szechuan as special tributes to the emperor in Peking. Due to their hardiness, their ability to tolerate a wide range of environmental conditions, their ease of propagation, and their flowering late in the spring season, the species of *Philadelphus* have become garden favorites, especially in the northern hemisphere.

By the latter part of the nineteenth century, forms of both Asiatic and American origin were established in various European gardens. Much was written about them, and very many binomials based on these exotic forms were published. Sometimes several or even up to a dozen different names were assigned to specimens taken from plants of the same origin. Some of the individual authors had only limited material for purposes of comparison, and others lacked specimens from the type localities. Thus it was inevitable that specific names were multiplied and much confusion resulted. In addition, clerical errors in recording names and in labeling living plants and preserved material provided further complication. In

some cases proposed new species were accredited to regions remote from their actual place of origin. Naturally different names came into use for species which not even a specialist could distinguish, and at the same time a single name may have been applied to very different species. Both botanists and horticulturists have complained of this nomenclatural confusion, yet since 1896 there has been no monographic work for the clarification of the entire group. Only scattered papers treating selected species or isolated groups from certain areas have been published. Actually, the lack of uniformity in selecting diagnostic characters by different authors has created further confusion. Thus it is that a practical scheme for the classification of the numerous species in the light of modern taxonomic knowledge and under the regulations of the accepted code of nomenclature is an urgent need.

Unaware of the difficulties in identifying species of this genus, I tried to name some unstudied Chinese material in the Arnold Arboretum herbarium. To my surprise, I was unable to find a workable key which could enable me to distinguish the Asiatic forms. After studying all the original descriptions I found myself even more confused for most of them are so meagre and the characters indicated are so generalized that one description often applies to any one of a number of obviously different species. I turned to more experienced taxonomists and horticulturists for advice and was warned that the species of *Philadelphus* have long been a botanical problem, and it would be wise for me to leave them alone. Though inexperienced in the group and perplexed by the confusion, I had the conviction that the man-made disturbances in the classification of the group could be solved when a real knowledge of the plants themselves had been acquired. I thus commenced an intensive study of the genus involving both living and herbarium material. My hope was that by careful examination of a large number of herbarium specimens collected from various centers of the natural range of the species supplemented with firsthand observations on the living plants cultivated in the Arnold Arboretum, the general pattern of the evolution of the genus might be discovered, and a natural order of relationship of the diversified taxa within the genus might be outlined. Besides the material deposited in the herbarium of the Arnold Arboretum (A) and the Gray Herbarium (G) of Harvard University, large loans were obtained from the Bailey Hortorium of Cornell University (BH), the Chicago Natural History Museum (F), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the University of Tennessee (TENN), and the United States National Herbarium (US). In September 1952, after the annual meeting of the American Society of Plant Taxonomists which took place at Cornell University, I examined the *Philadelphus* collection of the Wiegand Herbarium of that University (CU) and incorporated the notes in my manuscript. With these specimens, vegetative as well as floral characters were carefully analyzed. One by one the characters of geographically remote yet morphologically close taxa were intensively studied. Variations in each character were plotted with due allowance

for changes that may be caused by the age and vitality of the plant as observed in cultivated forms. The more constant characters were distinguished from the variable ones, and thus what I believe to be the fundamental morphological characters essential to proper specific diagnoses were ascertained. At the same time due attention was also given to those characters which might be used to advantage in defining categories above or below the specific level. By using these categories as standards of differentiation, various components of the geographically distinct groups were again investigated. Taxa of the same level were placed in what I assume to be their proper status, and thus a simple scheme of classification expressing the phylogenetic relationship of different groups was constructed on the basis of morphological characters and geographic distributions. It is hoped that this scheme will not only illustrate certain principles in the evolution and distribution of the genus, but also be of some service to horticulturists and to botanists who are concerned with the identification of their *Philadelphus* material, and to cytogeneticists who are interested in the chromosome numbers and behaviors of the various forms of this genus.

In this study the determinations of the taxa are made by comparing the specimens with the types as far as they are available. Since over 40% of the binomials pertaining to this genus were based on cultivated forms with no type ever designated, and sometimes with no actual specimens preserved, material annotated by their authors or specimens prepared from plants cultivated in the gardens indicated in the original publication are used to substitute for the types. In cases like *P. inodorus* Linn. where the taxon was based entirely on a previously published plate and a pre-Linnaean description, specimens from the type locality which best matched the illustration and agreed with the description were selected for identification purposes.

My thanks are due not only to the curators of the herbaria mentioned in the foregoing paragraph for the use of the facilities in their herbaria and libraries or for generous loans of material, but also to Dr. E. D. Merrill for patiently going over a large part of the manuscript with many valuable suggestions, to Dr. C. E. Kobuski for helpful criticisms and suggestions, to Dr. I. M. Johnston for assistance in locating literature regarding North American species, to Dr. K. Sax for consultations on cytogenetic and hybridization problems, to Dr. D. Wyman for the unselfish sharing of his profound knowledge of the living plants as well as the records of the cultivated forms on the grounds of the Arnold Arboretum, to Miss E. E. Upham for her patience in answering my numerous questions concerning both English and Latin, and to Mr. H. Howard for the photographs. I am also indebted to Dr. G. Taylor, Keeper of Botany at the British Museum and Dr. Charles Baehni, Director of the Conservatoire et Jardin Botaniques, Genève. With the help of Mr. Exell, the former gave me a detailed description of the nature of the pubescence on the hypanthium, disk and style of the type of *Philadelphus coronarius* Linn. in the Linnaean Herbarium. Through Professor E. D. Merrill, the

latter sent me the photographs of Schrader's manuscript and drawings together with the photocopies of the types of Schrader's species as published in De Candolle's *Prodromus*.

HISTORY

The first written account of a plant belonging to *Philadelphus* is found in a Chinese poem of the eleventh century describing the fragrance, color and contrast of the white flower with the green foliage, thus: "Herbs for color, trees for shape; None in fragrance to this [*Philadelphus*] compare. Like white foam in a sea of green, Unique among the shrubs it has been." Although this passage, like those of Gerarde, Clusius, Bauhin and other pre-Linnaean authors pertaining to the plant, is nomenclaturally of no importance to modern taxonomists, it nevertheless indicates the antiquity of man's knowledge of the *Philadelphus*.

By the time of Linnaeus, *Philadelphus* had already become a widely cultivated plant in European gardens. In pre-Linnaean literature it appeared as *Syringa* Tournefort, *Frutex coronarius* Clusius, or *Philadelphus* Athenaci et Rivinii. Linnaeus established the genus in 1737 and validated it in 1753. He recognized two species, *P. coronarius* and *P. inodorus*, and distinguished them by their leaf margins. Accordingly, the former species is characterized by its subdentate leaves and the latter by its entire leaves. The fresh material in the gardens of Clifford and Uppsala provided Linnaeus firsthand information about *P. coronarius*. Judging from the material preserved in the Linnaean Herbarium, he correctly identified it as representing Clusius' *Frutex coronarius*. Of the second species, he saw no specimen. His binomial was based wholly on the Catesby description and plate which in turn was based on material observed at the Savannah River region on the border of South Carolina and Georgia.

From the time of Linnaeus to that of A. P. de Candolle, botanists who were interested in *Philadelphus* had their studies limited to the few species of European and American origin, especially the cultivated forms. Miller in 1768 added one dwarf species and a variety with variegated leaves. As he had a larger collection of the living plant belonging to this genus, he perhaps acquired a more intimate knowledge of the group. He had seen sterile specimens of *P. inodorus* Linn. which he raised from cuttings sent him by Dale from Carolina. As these plants were killed by frost when two years old, his records on the height of the plant, the color of the flower and the size of the fruit were probably abstracted from Catesby's accounts. Willdenow in 1809, on the basis of material cultivated in the Botanical Garden of Berlin, described *P. grandiflora*, distinguishing it from *P. inodorus* Linn. by its prominently toothed leaves. About that time, *P. inodorus* Linn. was also in cultivation in a few gardens in England. Sims in 1812 on the basis of a specimen sent him by Whitley of the Fulham Nursery prepared a colored plate and a description for that species.

During this period, with the exception of Nuttall and Michaux, authors

on American flora had a very dim concept of the published species of American *Philadelphus*. Walter (1788) in the *Flora Caroliniana* presented a very general account of *P. inodorus* Linn. After comparing his statements about this species with that of Linnaeus, one has a feeling that he had never seen a specimen of it for he used even the same wording as Linnaeus. Michaux, being a true field naturalist, had seen the plant and in his *Flora Boreali-Americana* published in 1803 he used hitherto unknown characters about the long acuminate sepals, suboval petals and elongated undivided style for distinguishing *P. inodorus* Linn. Pursh in 1814 recognized four species, one of which, *P. lewisii*, was new. According to the material he cited, he probably had not seen any *P. inodorus* Linn. in America. His description was based on Sims' illustration and the cultivated material in England. Elliott in 1821 admitted that he had seen no specimen of *P. inodorus* Linn. in the various collections of dried plants which he had examined. He further stated that the plant was so rare in nature that no botanists in his day had seen it in the woods.

Nuttall in 1817 described *P. hirsutus* on the basis of his own collection from the bank of the French River near Warm Springs, Tennessee. His description of the species indicates that he was a man of keen and accurate observations and consequently his treatment gives the truest picture of the genus up to his time. He recognized four species. As three of them were American in origin, he was led to conclude that *Philadelphus* is "a North American genus, with the exception of *P. coronarius*." With our present knowledge of the genus, there is a great deal of truth in this statement, for not only the largest numbers of species of the genus occur in North America, but the principal morphological changes of the group are also found here.

Schrader was the first man who attempted to study the entire genus extensively. His dissertation on *Philadelphus* with illustrations which has been cited by De Candolle and Loudon has never been published. The manuscript is preserved in the Conservatoire et Jardin Botaniques, Genève. Part of it was incorporated by De Candolle (1828) in his *Prodromus* III. After Schrader's death, in the "Reliquiae Schraderianae" published in Linnaea (1838), an improved form of that dissertation appeared again, but without illustration. In the manuscript as well as the latter paper he included nine species and four varieties of *Philadelphus*. Unfortunately his material was largely limited to the forms then cultivated in European gardens. Having no access to specimens representing species already described by American botanists, he created several synonyms. Moreover, he accepted garden sports or hybrids as representing species and thus created additional confusion. He divided the then known species into two sections on the basis of the habit and the inflorescences, but assigned no sectional names to them. In the section "Caulibus crassioribus strictis, floribus racemosis" he recorded five species and three varieties. The rest were placed in the section "Caulibus tenuioribus virgatis laxis, floribus solitariis ternisve." Schrader's conclusions, whether correct or incorrect,

were followed by European botanists and horticulturists for over half a century.

De Candolle in 1828, using Schrader's manuscript as a standard, published a comprehensive treaty on the genus. He recognized eleven species and three varieties. For the three extra American species not included in Schrader's manuscript, he simply annexed them to Schrader's order and placed them all in the slender-stemmed and solitary-flowered group. This represents a very indiscriminate treatment, for closely related species like *P. coronarius* Linn. and *P. lewisii* Pursh, which are alike in their habit and inflorescences, were placed in separate sections.

Loudon in 1833 in *Arboretum et Fructicetum Britannicum* gave an illustrated comprehensive account of the genus. He recognized ten species and four varieties, placing them in two sections. In the "Stems stiff and straight. Flowers in Racemes" section he included six species and four varieties and in the "Stems more slender, rambling, twiggy and loose. Flowers solitary, or 2 or 3 together" section he had four species. In this classification what we now interpret as inseparable entities, like *P. inodorus* Linn. and *P. grandiflorus* Willd., were placed in different sections.

Philadelphus from Asia and Central America did not appear in botanical literature until the eighteen thirties. Wallich was the first person to discover a species of *Philadelphus* from Asia. In 1831 he named the specimens procured from Gossainthan, Sirmore and Kamaon as *P. tomentosus* and *P. triflorus*. G. Don in 1832 validated the first binomial by giving it a description and Royle in 1839 prepared a colored plate for this Himalayan taxon.

Schlechtendal in 1839 on the basis of Schiede's collection from Jalapa and Ehrenberg's collection from Carmen described *P. mexicanus*, the first species of *Philadelphus* from Central America. About the same time, Bertoloni (1840) published an illustrated account of a Guatemala species under the name *P. myrtoides*, a species which marks the southmost limit of the spontaneous distribution of the genus.

A. Gray in 1849 on the basis of Fendler's collection from Santa Fe Creek, New Mexico, published *P. microphyllus*, the first known xerophytic species. The plant was introduced to Europe in 1883 and hybridists there took advantage of its low habit and very agreeable fragrance and in the autumn of 1887, the Lemoine Nursery of Nancy, France, put into commerce a novelty under the name, *P. lemoinei*, which was announced to be the result of a cross between the American small-leaved species, *P. microphyllus* Gray and the much cultivated European species, *P. coronarius*.

Lindley and Paxton in 1852 published *P. satsumi* Sieb., the first known species of *Philadelphus* from Eastern Asia, on the basis of both living material introduced and the herbarium specimens prepared by Siebold from Japan. Ruprecht in 1856, in a paper of Maximowicz on the important trees and shrubs of the Amur Region, described *P. tenuifolius*, the first known species of *Philadelphus* from the Eastern Asia mainland. A year later in a discussion about *P. tenuifolius* he accidentally published *P. pekinensis* which became the first known Chinese species in the genus.

By the middle of the nineteenth century *Philadelphus* introduced from America and Asia were cultivated under thirty odd names in European gardens. Botanists and growers began to be conscious of the confusion and tried to clarify the nomenclature and to identify the plants. The general tendency shows a lumping effort. Koch in 1859 in an article titled, "Notes on the Genus *Philadelphus*," first published in Germany and then translated by De Borre into French, recognized 16 species. Ten years later, in his *Dendrologie* he reduced the number to 11 species. His species concept was rather vague and he clearly erred in making species of American and Asiatic origin conspecific entities. His work created confusion rather than clarification. Maximowicz in 1867, in a "Revisio Hydrangearum Asiae Orientalis," treated all the species of *Philadelphus* that had racemose inflorescences, including those from Europe, Caucasus, Himalayan Regions, eastern Siberia, northeastern China, Japan and North America, as varieties of *P. coronarius* and thus created a large number of synonyms.

Koehne was the best authority of the group, and he was careful and keen in his observations. Unfortunately the diagnostic characters he chose to delimit subsidiary groups between the species and the genus do not at all well cover the characters of the species involved, and his arrangement proved to be impracticable. In 1893 he selected the exfoliation of the bark as the most important character for distinguishing major groups. He divided the genus into the *Corticatae*, including those species with closed bark and the *Decorticatae* containing those with exfoliate bark. Realizing this character to be unreliable and the scheme not workable, three years later, he selected the size of the stigma as the distinguishing character for dividing major groups. On this basis he proposed two sections, the *Poecilostigma* and the *Stenostigma*. His section *Poecilostigma* represents a conglomeration of phylogenetically unrelated species. This section was subdivided into three subsections, the *Gemmati* with exposed buds, the *Microphylli* containing species with inclosed buds, small leaves and united and more or less separated stigmas; and the *Speciosi* including species with inclosed buds, large leaves and separated broad stigmas. His section *Stenostigma* represents species with inclosed buds and separated narrow stigmas. This was subdivided into four subsections; the *Paniculati* with paniculate inflorescences, the *Gordoniani* with racemose inflorescences, decorticate branchlets and late flowering individuals, the *Satsumani* with racemose inflorescences, decorticate branchlets and early blooming individuals, and the *Coronarii* with racemose inflorescences, corticate branchlets and usually early flowering individuals. In this classification Koehne failed to give a single character which holds true for the *Poecilostigma* as a section, and for the demarcation of the *Stenostigma* he gave two characters, that is, the narrow stigmas and the inclosed buds. At first his statement seems to be acceptable. But as one examines the species that Koehne placed in the *Stenostigma* section, one finds that this section cannot stand as a taxonomic unit, for the first listed species *P. californicus* Benth. has exposed axillary buds, a character which is not

supposed to exist in the section. Moreover, the differences in the size and shape of the stigmas between species of this section is just as great as are those in *Poecilostigma*. As to the characters he chose for distinguishing subsections they are not strong enough even for delimiting species. The manner of the peeling of the bark and the time of blooming are subjected so much to the environmental changes that they are not of much value except for distinguishing closely related garden forms planted in similar conditions. Although Koehne's system of classification has been followed by many authors including Engler in his treatment of the genus in the second edition of *Die Natürliche Pflanzenfamilien*, it is not adopted in this study, for it represents a more artificial and less phylogenetic system.

The beginning of the twentieth century seems to mark a new tendency in the study of *Philadelphus*. Botanists began to show interest in the group on a regional basis. Beadle in 1902 concentrated in a study of *Philadelphus* of the southeastern United States and proposed three new species and one new variety from the homeland of *P. inodorus*. His findings were the basis for the treatment of the genus in Small's *Flora of the Southeastern United States* (1903, 1913) and the *Manual of the Southeastern Flora* (1933) of the same author. He introduced the shape of the base of the capsules for distinguishing species. Thus he characterized *P. inodorus* as a species in which the base of the fruit attenuates into the pedicel and distinguished his new species, *P. gloriosus* from *P. inodorus* by the abruptly contracted fruit base. This character has never been used by any other botanist in the classification of *Philadelphus*. As the shape of the base of the capsule in this genus depends upon the fullness of the fruit which in turn depends partially upon the environmental conditions and partially upon the time when the specimens are collected, it has little value for specific identification.

Rydberg in 1905 prepared a comprehensive treatment of the genus for North America. The principal diagnostic characters he used were the presence or the absence of hairs on the style and disk which he called the upper free part of the ovary, the number of flowers on a flowering branch and the size of the leaf. He recognized 36 species, 10 of which were new. In the key, he grouped those species into six subdivisions, the *Californici*, *Coronarii*, *Grandiflori*, *Hirsuti*, *Microphylli* and *Mexicani*. His work indicates his ability in recognizing differences, and most of his species are good ones. Although some modern botanists may prefer to place the taxa he recognized in subspecific rank, that is only a matter of opinion which does not affect those taxa being distinct entities.

Nakai in 1915 considered the species of Japan and Korea, recognizing seven species, two of which were new. On the basis of bark characters of the second year's growth, whether closed or exfoliate, he raised two of Koehne's subsections into sections. In *Satsumani* he placed a single species, *P. satsumi* and in *Coronarii* he placed all the other species.

Rehder (1920, 1927, 1940, 1949) considered chiefly the cultivated species and varieties. In 1927 he subdivided the genus into six groups:

1. Gordoniani, 2. Sericanthi, 3. Coronarii, 4. Speciosi, 5. Microphylli and 6. Gemmati. Later (1940) he definitely designated these groups as Series. The characters he employed in the key were the number of flowers on a flowering branchlet, the pubescence on the hypanthium, the color of the calyx, etc. He was at times inconsistent when, as an example, he separated a group of species by the pubescence on their hypanthia, yet under certain species of this category he recognized varieties with glabrous hypanthia, as in the case of *P. pubescens* Loisel. var. *intectus* (Beadle) Moore. The diagnostic characters for a series do not always agree with his key characters, as in the case of *P. purpureo-maculatus* Rehd. In the text, he placed this species in series Microphylli which is characteristically a taxon with hidden buds while in the key it is placed under the category of exerted buds. His series concept impresses me as rather vague for in some cases a series consists of species different from each other in many respects. Thus in Series Gordoniani, he placed *P. californicus* Benth. with paniculate inflorescence, glabrous hypanthium and exposed buds as well as *P. pubescens* Loisel. with racemose inflorescence, pubescent hypanthium and inclosed buds; and in Series Sericanthi he placed *P. sericanthus* Koehne with pubescent hypanthium and also *P. delavayi* L. Henry with glabrous hypanthium. Moreover, in some cases morphologically inseparable and geographically closely affiliated taxa like *P. tomentosus* Wall and *P. delavayi* L. Henry are allotted to different series. Rehder's identification formed the basis for Bangham's chromosome count of the genus, and his taxonomic units were adopted by Janaki Ammal in her discussion on the classification and geographical distribution of *Philadelphus*. Rehder's material was restricted to the cultivated species of the temperate regions. This geographical limitation combined with the short-comings of his classification consequently affected the value of the conclusions drawn by the cytologists.

Hitchcock in 1943 studied the American xerophytic species. His work contributes materially to an understanding of the group. He considered four species and thirteen subspecies, all placed in what he called the Microphylli group. According to him, these small-leaved species, "As a unit . . . are readily distinguished from all other North American species of *Philadelphus*, yet it is quite apparent that they have been derived from, and are very closely related to, certain species of the *Mexicani*." I have carefully examined all the taxa that Hitchcock considered as representing a single group, and I can only conclude that this "group" includes heterogeneous elements. The small leaved character impresses me as being misleading. The comparative study of the morphological characters and geographical distribution of all the species of the genus indicates that the elements native of the region considered by Hitchcock are end products of evolution stemming from two or three directions. It is true that three of the four species in Hitchcock's treatment, *P. serpyllifolius* Gray, *P. purpusii* Brandeg. and *P. mearnsii* Evans are related to the Mexican elements. But *P. microphyllus* Gray and its related taxa are surely distant from them in their phylogenetic relationships. In my

judgement his conclusion on *P. microphyllus* Gray being a derivative of *P. purpusii* Brandeg. is too arbitrary. Before me there are several specimens from the Northern Rocky Mountains, chiefly Montana, with characters intermediate between *P. lewisii* Pursh and *P. microphyllus* Gray. The size, form and texture of the leaves and the size of the flowers of these specimens are typical of *P. microphyllus* Gray, but some, or rather, most flowering branchlets possess five flowers which is characteristic of *P. lewisii* Pursh. These spontaneous intermediate forms are good evidence of the origin of *P. microphyllus* Gray and its related species. Nevertheless, Hitchcock's paper takes high rank among all those published on the genus. I believe that it was unfortunate that his studies were limited to the small-leaved forms, for leaf size is indeed an unreliable character, and generalizations can scarcely be made except on the basis of a critical study of all species of the genus.

From the late 1920s up to the present the discoveries of botanists in fields other than taxonomy have broadened our knowledge of *Philadelphus*. Bangham in 1929¹ published the result of his observation on the chromosome number of the genus. Janaki Ammal in 1951² treated the subject in greater detail and discovered triploid and aneuploid individuals in garden forms. These findings will eventually help breeders to obtain better garden forms, for by suitable mating of parents of known chromosome compositions, better hybrids with triploid, or perhaps tetraploid or aneuploid chromosome makeups can be induced. As in many ornamental plants some extra chromosomes often enhance their horticultural merits.

Chaney in 1939 and Condit in 1944³ confirmed the occurrence of fossil *Philadelphus* in the middle upper Miocene. The fossil *P. nevadensis* (Knowlton) Chaney resembles the leaves of *P. lewisii* Pursh which now occurs in northwestern United States. This discovery advances our understanding of the present distribution of the species in this genus.

EVALUATION OF MORPHOLOGICAL CHARACTERS IN THE CLASSIFICATION OF THE GENUS

In the historical review of *Philadelphus* studies I have noted that the habit of the plant, the color and exfoliation of the branchlets, the position of the buds, the size, texture, dentation and indumentum of the leaves, the inflorescences, and the floral parts have all been used either as major or minor diagnostic characters in the classification of the species of the genus. Individual authors have stressed different points and consequently their systems of classification lack uniformity. In the following discussion an attempt is made to evaluate characters stressed by others as well as to add certain fruit and seed data.

¹ The Chromosomes of Some Species of the Genus *Philadelphus*. Jour. Arnold Arb. 10: 167-169. 1929.

² Chromosomes and the evolution of Garden *Philadelphus*. Jour. Royal Hort. Soc. 76: 269-275. 1951.

³ R. W. CHANEY, Pliocene Floras of California and Oregon, Carnegie Inst. Washington Publication 553. p. 79. pl. 16. fig. 2. 1944.

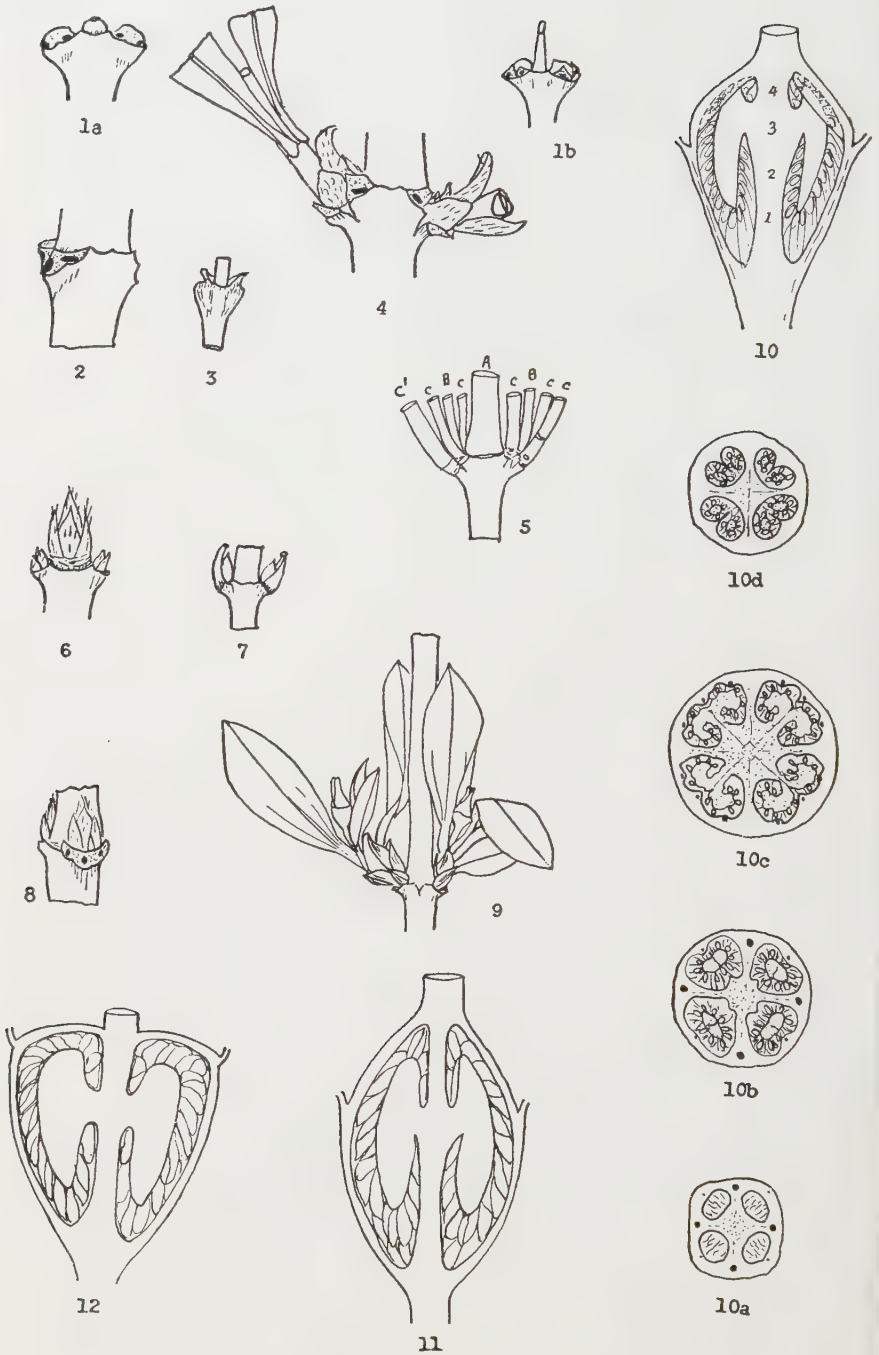
Habit: The habit was used as a principal criterion for separating major groups by early authors like De Candolle and Schrader. As our knowledge of the genus increased, the importance of the habit in the classification of *Philadelphus* gradually decreased. Judging from plants cultivated in the Arnold Arboretum, there seems to be no correlation between the habit of the plant and the other morphological characters such as the position of the buds, or the number of the flowers. Moreover, the habit is often affected by the environmental conditions and the age and vitality of the plant. Possibly the habit, such as upright tall stiff shrub, low widely spreading shrub with twisted branchlets, low compact shrub with upright branches or moundlike tall shrub with arching branchlets, may be used for recognizing special horticultural forms, varieties or even species, but it should not be used for distinguishing taxa above these ranks.

Branchlets: In general practice, a few branchlets constitute the only material a herbarium taxonomist may have for purposes of study and identification. Regarding the branchlets of *Philadelphus*, my discussion will be carried on under the headings of the second year's growth, current year's growth, the axillary buds, and the adventitious growth.

The color and exfoliation of the bark of the second year's growth, whether closed or exfoliate, has been employed by Koehne, Rehder and others for distinguishing species or even taxa of higher rank. It is true that the bark of certain species such as *P. pubescens* Loisel. and its related forms are prevailing gray. But that of the other species is of various shades of brown, from ash-brown to reddish chestnut. In some species the bark exfoliates in sheets. In others they slowly wear off. It seems to be apparent that the size and the age of the shoot, the rainfall of the growing season, and the amount of snow in the preceding winter are all contributing factors effecting the exfoliation of the bark. Often different shoots on the same plant differ in the degree of exfoliation. As the herbarium specimens represent only very small portions of an individual plant, the actual selection of specimens may govern the evident exfoliation and bark color very materially. When only a few specimens are available, one may interpret the bark color and exfoliation of the second year's growth as forming a definite criterion for species delimitation, but when many specimens from the same general area are examined, the intergradations in color and exfoliation should convince any one that these characters are of little value in recognizing species.

The current year's growth of all species of *Philadelphus* are of two kinds, the sterile shoots bear leaves only, and the flowering shoots each of which bears one to three (or very rarely more) pairs of leaves and a terminal flower or a cluster of flowers. The sterile shoots are more vigorous and their leaves are larger and comparatively more dentate than are those of the flowering branchlets. The bud position on these shoots is very constant.

In one group, the buds are hidden in nodal pouches at the ends of the petioles (Pl. I, fig. 3). When the leaves fall, these buds are covered by



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the abscission layers (Pl. I, fig. 1a, 1b, & 2). As these buds unfold, they burst open the abscission layers (Pl. I, fig. 4) which persist for a long time at the base of the new branchlets. All the plants with such hidden axillary buds bear no terminal buds. Their shoots are determinate. All the Old World species of *Philadelphus* and many of those of the New World are characterized by such hidden buds and determinate branchlets.

In contrast, other species bear prominent conical axillary buds on their sterile and flowering shoots at anthesis (Pl. I, fig. 7, 8). In general, nodes bearing these buds are strongly curved below the insertion of the leaves, while those with hidden buds are but slightly curved. It is doubtful if latitude and temperature have any effect on the production and size of the exposed buds. Thus, *P. hirsutus* Nutt. is a native of the southern Appalachian Mountains, but when cultivated in Boston, which is nearly seven degrees higher in latitude than the original home of the species and Boston has an average annual minimum temperature 10–15 degrees lower than Nashville where the plant grows wild, its axillary buds at anthesis are just as prominent as are those on the Tennessee specimens. Moreover,

PLATE I

1. Shoot apex of the determinate type ($\times 4$, from fresh material collected in the Arnold Arboretum, Jan. 20, 1952). 1a. *P. coronarius* with the lateral buds completely covered by the abscission layer. 1b. *P. microphyllus* with the lateral buds more or less unfolding, the dead terminal portion of the branchlet is more prominent here. 2. Node of *P. delavayi* after the leaves have fallen, showing the lateral buds covered by the abscission layer ($\times 4$, Rock 16637). 3. Node of *P. maculatus* with the ends of the petioles attached, showing prominent nodal pouches containing the buds; the curves below the insertion of the leaves are gentle ($\times 4$, Mueller 2213). 4. Node of *P. delavayi* with the axillary buds unfolding and each abscission layer has burst open ($\times 3$, Rock 16173). 5. Node of a sucker; A, with two branches B, developed from normal axillary buds and six branches developed from adventitious buds. Five of the six are flowering shoots C, and one is a vegetative shoot C'. 6. Shoot apex of the indeterminate type, *P. hirsutus*, with a large terminal bud and two small lateral ones ($\times 4$, from fresh material collected in the Arnold Arboretum on Jan. 20, 1952). 7. Node of *P. texensis* with the petioles on, showing the exposed axillary buds, the curves below the insertion of the leaves are sharp. ($\times 4$, Reverchon 1523). 8. Node of *P. hirsutus* after the leaves have fallen, showing two lateral buds exposed ($\times 4$, fresh material collected in the Arnold Arboretum, Jan. 20, 1952). 9. Node of *P. mearsii* after the buds are unfolded. The unfolding of the buds does not affect the leaf-scars ($\times 5$, Palmer 11492). 10. Longitudinal section of a fruit of *P. inodorus*, 1 week after anthesis, showing the attachment of the placentas which are above the insertions of the sepals ($\times 10$). 10a, 10b, 10c, and 10d are transverse sections of the above cut through the points 1, 2, 3, and 4. 10d appears 8-locular. 11. Longitudinal section of a fruit of *P. microphyllus*, 2 months after anthesis, showing the attachment of the placentas which are about the same level as the insertions of the sepals ($\times 10$). 12. Longitudinal section of a mature fruit of *P. hirsutus* showing the attachment of the placentas which are below the insertions of the sepals ($\times 10$).

such plants often bear strong terminal vegetative buds (Pl. I, fig. 6), therefore their shoots are indeterminate. All the species with exposed buds occur in the New World.

The presence or absence of exposed buds is not only constant, but the buds are also very easy to detect. As long as the leaves are mature, no matter whether the branchlets be sterile or fertile, the buds are evident. The morphological constancy and the geographical coincidence indicate that the position of the buds whether hidden or exposed, is a very good character for separating major groups in *Philadelphus*. Accordingly, in this study I take this character as one of the key categories for delimiting the subgenera of the genus.

All species of *Philadelphus* produce adventitious buds at the basal portions of their principal stems or along the upper parts of their branches. In the first case, the buds develop into strong sterile shoots which give rise to flowering branchlets in the following year. In the second case, the buds may develop into a weaker sterile shoot (Pl. I, fig. 5, c'), or usually they form weak flowering branchlets, (Pl. I, fig. 5, c). The leaves of such shoots are generally smaller and the flowers fewer than are those developed from normal buds. The presence of a number of such small flowering branchlets gives the stem somewhat the appearance of a brush. A branch with multiple branchlets at its nodes should always be taken as a sign of old age and reduced vitality in the plant.

Leaves: Authors of the first few species of *Philadelphus* relied chiefly on leaf characters for distinguishing them. Thus Linnaeus distinguished *P. inodorus* from *P. coronarius* by its entire leaves and Willdenow distinguished his *P. grandiflorus* by its dentate leaves. When only a few specimens are compared, there may be seemingly marked differences in the size, shape, texture, venation and margin of the leaves. But when a large number of specimens are available for comparative study, the gradual changes exhibited in these respects prove that what various authors such as Schrader, Koch, Maximowicz, and Rydberg accepted as differential specific characters are not constant. In fact, there is little difference in the size and shape of the leaves of the species of *Philadelphus* of any single area, and also often even between species from distant regions with similar climatic conditions. The differences that existed in the size, shape, texture and margin of related species may also occur as modifications among representative specimens from the same species differing only in age and vigor. Therefore the size and shape in the leaves can only be used as supplementary criteria for distinguishing varieties or garden forms and occasionally even species when it is correlated with characters furnished by flowers and fruits.

The leaves on the sterile shoots and those on the flowering shoots of an individual plant differ in size, shape, apex and margin. In general the leaves on the sterile shoots are larger, more acuminate at the apex, more coarsely dentate at the margin, more pubescent on the surface and even broader at the base than are those on the flowering shoots. Yet, leaves of a flowering shoot developed from an adventitious bud are always much

smaller, more acute, more subentire and more glabrous than are those developed from normal buds. One judges that the age of the plant, the vigor of the shoot, the available water supply may be reflected in the leaves of *Philadelphus*. For this reason, leaf characters based on these aspects should not be employed for the delimitation of taxa above varieties or garden forms.

The nature and the density of the indumentum on the leaf surfaces are rather constant as to leaves on comparable shoots of a species. They usually correlate with certain flower characters, therefore may be used as auxiliary criteria for distinguishing species or categories of even higher rank, such as section and series.

Inflorescences: *Philadelphus* as a genus is characterized by determinate terminal inflorescences, each with 1 or 3 flowers at the last node, and none, one, rarely two single flowers, or very rarely a cyme in the axil of a bract or a leaf on each side of the succeeding nodes. When the succeeding node bears no flower, the branchlet has solitary or ternate flowers. When the succeeding nodes bear flowers the plant has racemose or paniculate inflorescences, depending on the number of flowers in the leaf axils. In many species the bracts are small and caducous. Since De Candolle in 1828 used the term raceme to describe *P. coronarius* Linn. and its related species, it has been used in reference to those species with a terminal cluster of flowers in all major treatments of the genus. But actually when the order of blooming is taken into consideration, none of the *Philadelphus* species really bear true racemes. In this genus, the first opened flower always prohibits the elongation of the flowering shoot and limits the formation of more flower buds. The figures on Plate II actually represent the number of flowers and their relative developments on the branches of *P. californicus* Benth., *P. pubescens* Loisel., *P. lewisii* Pursh, *P. pekinensis* Rupr., *P. inodorus* Linn., *P. microphyllus* Gray, *P. falconii* Sarg., *P. karwinskyanus* Koehne, *P. myrtoides* Bertol., *P. mexicanus* Schlecht., *P. hirsutus* Nutt. and *P. serpyllifolius* Gray. In each case the flowers at each node behave as an independent unit. In cases where many flowers are formed at the end of the flowering branch the terminal one always opens first. Such inflorescence is a determinate raceme or a panicle.

Philadelphus inflorescences may be roughly arranged in six general types, the paniculate, the determinate-racemose, the pauciflorous, the ramiferous, the mexicanus, and hirsutus types. The paniculate type includes inflorescences composed of simple or more or less compound cymes (Pl. II, fig. 1). It is represented by *P. californicus* Benth. and *P. cordifolius* Lange. The determinate-racemose type is the commonest type of inflorescence in the genus. It is best represented by *P. pubescens* Loisel. and *P. lewisii* Pursh in the United States, *P. satsumi* Sieb. of Japan, *P. tenuifolius* Rupr. of the Amur Region, *P. pekinensis* Rupr. and all the other Chinese species, *P. tomentosus* Wall. of the Himalayan Region and *P. caucasicus* Koehne and *P. coronarius* Linn. of Caucasia and southwestern Europe. It consists of 3, or very rarely 1, or occasionally in *P. coronarius* Linn. 5, terminal flowers and several pairs of axillary ones at the suc-



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ceeding nodes (Pl. II, fig. 2-5). Sometimes, as in *P. coronarius* Linn., a pair of flowers may appear in a single leaf axil. The upper axillary flowers are often subtended by bracts which fall early in the flowering season. The lower axillary flowers are in general subtended by normal leaves. Great variations exist in the number of flowers in a cluster, the length of the central axis and the size of the bracts in specimens representing a species or sometimes even from a single plant. This is especially true in *P. lewisii* Pursh and *P. pekinensis* Rupr. It seems that the age and vitality of the shoots which give rise to the flowering branches are the controlling factors for such modifications. There are certain garden forms characterized by a predominantly short flowering axis. In such cases the clusters appear rather compact (Pl. II, fig. 4, 5). There are certain species which bear loose determinate-racemes. In such cases the lower two pairs of flowers are borne in the axils of normal leaves (Pl. II, fig. 2, 3); the inflorescences of *P. pubescens* Loisel. and *P. intactus* Beadle are typically of such form.

The pauciflorous type consists of inflorescences with one or three terminal flowers on shoots devoid of exposed axillary buds. This type is best illustrated by *P. inodorus* Linn. and *P. microphyllus* Gray (Pl. II, fig. 6, 7) and their related species. In certain garden forms, the lateral flowers of this type may be replaced by two cymes with elongated peduncles. In such cases, a true dichasium is formed (Pl. II, fig. 8).

The ramiferous types of inflorescences are depauperated panicles. They may appear as racemes or panicles, but each individual flower is on a short pedicel jointed to a woody axis. Thus each flower stalk is morphologically composed of a peduncle and a pedicel. In *P. myrtoides* Bertol. the peduncles of the lower flowers are as long as those of the upper one and the inflorescence appears more or less racemose, but the individual pedicels are jointed (Pl. II, fig. 10). In the more ramified form, as represented by *P. karwinskyanus* Koehne, the inflorescence is composed of elongated lower branches (Pl. II, fig. 9) and shorter upper ones, and it appears like a panicle. Some of the lower branches even bear axillary buds on their basal nodes.

The mexicanus type has one or three terminal flowers on short but jointed stalks, as found in *P. mexicanus* Schlecht. Such an inflorescence

PLATE II

TYPES OF INFLORESCENCE IN PHILADELPHUS (all $\times \frac{1}{2}$). 1. The PANICULATE TYPE, *P. californicus* (Abrams 4649). 2-5. The DETERMINATE-RACEMOSE TYPES. 2. *P. pubescens* (AA 2221). 3. *P. lewisii* with 3 terminal flowers (Thompson 10522). 4. *P. lewisii* with 1 terminal flower (Engberg, June 19, 1905). 5. *P. pekinensis* (Hers 2515). 6 & 7. The PAUCIFLOROUS TYPE. 6. *P. inodorus* (AA 4159-1). 7. *P. microphyllus* (Fendler 266). 8 TRUE DICHASIMUM, *P. falconeri* (Hu, June 14, 1951). 9 & 10. The RAMIFEROUS TYPE. 9. *P. karwinskyanus* (FGW 872). 10. *P. myrtoides* (Carlson 435). 11. The MEXICANUS TYPE, *P. mexicanus* (Standley 65124). 12. The HIRSUTUS TYPE, *P. hirsutus* (Palmer 35517). 13. The SERPYLLIFOLIUS TYPE, *P. serpyllifolius* (Cary 9435).

is probably a reduced or simplified compound inflorescence with the portion above the bracts representing the pedicel and the portion below the joint, the peduncle.

The *hirsutus* type, as represented by *P. hirsutus* Nutt. and *P. mearnsii* Evans, has inflorescences of solitary or ternate flowers on short flowering branches with exposed axillary buds (Pl. II, fig. 12, 13). Such inflorescence often develops from a terminal bud.

The type of inflorescence in *Philadelphus* is a definite and easily recognizable character. When correlated with the position of the buds, the form of stigma, the shape of fruit, and the appendages of the seed, the type of inflorescence can be employed as a very useful device for distinguishing sections of the genus as well as for assisting in placing the species in its phylogenetic position. In using the inflorescence in the classification of *Philadelphus* several essential points should be observed. (1) All the inflorescences of *Philadelphus*, no matter whether they are composed of a single flower, or three or five up to 20 flowers in simple or ramified branches, are borne at the end of current year's growth. In other words, they are all derivatives of individual buds which are usually axillary. (2) All of them are determinate inflorescences; that is, the terminal flower in each type opens first and they thus limit the elongation of the floral axis. (3) The type of inflorescence of a species is definite, but the number of flowers on each flowering branch is variable. A species with pauciflorous type of inflorescence may have some branches with a single flower, some with three and others with a true dichasium of seven or nine flowers. This variation seems to be a reflection of the environmental condition of the plant as well as the physiological state of the particular flowering branch. In the cultivated *Philadelphus*, good soil, sufficient water supply, proper pruning, vigor of the plant and the bearing year always induce a large number of flowers on a branch. In case of the determinate-racemose type of inflorescence the floral axis is always lengthened.

Rickett in 1944 discussed the inflorescences of *Philadelphus* at length. He used *P. coronarius* Linn., *P. californicus* Benth., *P. lewisii* Pursh, *P. argenteus* Rydb. and *P. hirsutus* Nutt. to illustrate a hypothesis that the terminal dichasium is ancestral in *Philadelphus*. He maintained that this primitive type can be found in *P. hirsutus* Nutt., and suggested that the present forms of the inflorescences of *Philadelphus* are evolved through the reduction of the terminal dichasium to a single flower as found in *P. argenteus* Rydb. Further reduction of the lateral flowering branches leads to the production of axillary flowers of *P. coronarius* Linn. This condensation is accompanied by a lack of dormancy in the new axillary buds, which open the same season as the leaves which subtend them. From flowering branches formed in such a way, derived the floral arrangement as seen in *P. lewisii* Pursh and also the thyrses of *P. californicus* Benth., the latter represents a condensation of the second order, that is, not only are a number of the original flowering branches laterally disposed on a central rachis, but several groups thus constituted are similarly disposed on the main axis of the thyrses. According to this hypothesis the

evolution of the inflorescences of *Philadelphus* has been brought about merely by reduction and condensation of the flowering branches. As I understand the morphology of *Philadelphus*, certain assumptions accepted by Rickett apparently do not conform to what are found in nature. First he selected the inflorescence of *P. hirsutus* Nutt. to represent the ancestral form, but this species is morphologically highly specialized and its low point of placentation and its ecaudate seeds all indicate its advanced position in the evolution of the genus. Secondly, he maintained that the inflorescence of *P. argenteus* Rydb. is a derivative of that of *P. hirsutus* Nutt., but these two species are phylogenetically very remote. They belong to different subgenera. Thirdly, the condensation processes that he assumed to take place between *P. argenteus* Rydb. and *P. coronarius* Linn. and between *P. lewisii* Pursh and *P. californicus* Benth. involve more than a single year's growth. The plant part he took from *P. argenteus* Rydb., or *P. lewisii* Pursh to illustrate his principle represents two year's growth with twigs bearing buds on part of old wood and what he took from *P. coronarius* Linn. or *P. californicus* Benth. represent a single year's growth, originated from a single winter bud. When he assumed that the branch of *P. lewisii* Pursh with a number of flowering branches laterally disposed to be condensed on a central rachis to form an inflorescence corresponding to those of *P. californicus* Benth., he overlooked the age differences of the two elements involved. It is not possible within the organization of the plant to attain such assumed condensation. Moreover a shoot of *P. lewisii* Pursh that bears laterally disposed flowering branches never possesses a terminal bud, so that it is impossible for that shoot to be condensed on the main axis of the thyrses to form a paniculate inflorescence of *P. californicus* Benth. which ends with a terminal flower. Moreover, *P. coronarius* Linn. and *P. lewisii* Pursh have the same determinate-racemose type of inflorescence. When one takes into consideration all factors, it is unnecessary to invoke imagination to explain the evolution of the inflorescences of *Philadelphus*. Rickett was perhaps right in assuming the terminal dichasium as the ancestral type. He was partly correct in recognizing reduction and condensation as a process that brings about the various forms of inflorescences in *Philadelphus* but unfortunately he chose the inflorescence of *P. hirsutus* Nutt. to represent the primitive model. The most primitive type of inflorescence in *Philadelphus* is the pauciflorous type as found in the true terminal dichasium of a healthy vigorously growing flowering branch of *P. inodorus* Linn. Normally such dichasia may be reduced to three or a single terminal flower. The solitary or ternate terminal flower of *P. microphyllus* Gray and all its related species represents a comparatively stable stage of development of such reduced form. The reduction in the height of the plant, the size of the leaves, the number of stamens, the length of style and the size of the stigma all conform with the fact of such reduction in number of flowers. Multiplication as well as reduction, and some times a combination of both processes may have taken place in the evolution of the *Philadelphus* inflorescences. The multiplication in the number of

flowers which are produced in the leaf-axils of the succeeding nodes below the terminal one, gives rise to the determinate-racemose type, and further multiplication which involves the branching of the flowering pedicels gives rise to the paniculate type. The mexicanus type is another primitive model which is closely related to the pauciflorous type. The multiplication in the number of flowers and the ramification of the flowering branches of this type give rise to the ramiferous type. The hirsutus type is remote from all other types of *Philadelphus* inflorescence. Its slender pedicels with median or super median bracts, its irregular way of branching, and its appearance remind one of the inflorescence of certain *Deutzia*. It is probably derived from some form very remotely related to the mexicanus type but the linking form is not known in our present flora.

Pedicels: The length of the pedicels in *Philadelphus* varies considerably. The general tendency is, in the determinate-racemose type, the lower ones are longer than the upper ones, or in the pauciflorous types, the lateral ones longer than the central one. As a criterion for classification, this character has little value. Nevertheless, most species have pubescent pedicels. The nature and density of the trichomes on the pedicels of closely related species are sometimes employed as auxiliary characters for recognizing species or varieties.

Hypanthia: Part of the ovary of *Philadelphus* is fused to the receptacle. In this paper the term hypanthium is used to cover that part called the calyx tube by some authors. For the visible top portion of the ovary the term disk is used.

At anthesis, there is no appreciable difference in the shape and size of the hypanthia of closely related species. But the nature and density of the indumentum which persist in the fruit are very useful for specific identifications, or even for the delimitation of series. Most *Philadelphus* species have yellowish green hypanthia. Certain Chinese species have purplish ones. In such case, color may be used as a handy auxiliary character for identifying species or varieties.

Sepals: The sepals of *Philadelphus* are ovate, rarely deltoid, 4-20 mm. long, acuminate (rarely acute) at the apex. The relatively shortest sepals occur in *P. hirsutus* and the longest ones in *P. inodorus* and *P. mexicanus*. The length, shape and apex of the sepals have been employed by various authors for distinguishing morphologically similar and geographically intermixed species. The study of a large amount of material in this genus reveals that the natural population of any general area belonging to the same section exhibits very little variation in the size and shape of the sepals. Thus, in my opinion, they have no specific significance.

Corolla and petals: Characters of the corolla and the petals have been little used in the classification of the genus. One Central American species has been recognized for its pubescent petals, while another species of northwestern United States has been characterized by its pointed petals.

In shape and size the petals of various species are rather constant. They may be oblong, elliptic, suborbicular or lanceolate. The variations in the shape and size of the petals give the different appearance of the flowers.

Thus *P. inodorus* var. *laxus* (Schrader) S. Y. Hu has oblong petals, and its flowers are distinctly cruciform when fully open (Pl. III, col. 3). The petals of *P. inodorus* Linn. var. *grandiflorus* (Willd.) Gray are sub-orbicular, and consequently its flowers appear disciform (Pl. III, col. 1). is an important aspect for distinguishing varieties and garden forms, the of *Philadelphus*. It shows a considerable difference in the size, shape and appearance of the corollas in the genus. As the appearance of flowers is an important aspect for distinguishing varieties and garden forms, the size and shape of the petals may eventually have a more important role in demarcating entities subordinate to the species.

Stamens: There is noticeable variation in the number of stamens not only between different species or different plants which clearly represent a single species, but also between different flowers of the same plant. The forms possessing the most stamens are found in *P. inodorus* Linn. and its varieties where as many as 90 stamens have been observed. The smallest number of stamens observed is in *P. mearnsii* Evans where as few as 13 stamens have been counted. But variations in the number of stamens between different flowers on the same plant do exist. With the first cited example as few as 60 stamens and with the second species as many as 20 stamens have been observed. For demarcating morphologically closely related and geographically inseparable species the number of stamens does not seem to have much significance. But there apparently exists a general pattern of stamen number between morphologically different and geographically widely separated groups. Thus the native population of *Philadelphus* of the Southern Appalachian region with pauciflorous inflorescences have the highest stamen count which is between 60 and 90; the xerophytic plants of the southern Rockies with the pauciflorous type of inflorescences have an average count of 30 to 40, rarely as low as 24 or as high as 50 stamens; the native species of Central America with ramiferous inflorescences have 40 to 50 stamens and those with the mexicanus type of inflorescences have 36 to 44 stamens. The Old World species with racemose inflorescences generally have 25 to 35, rarely to 50 stamens. Garden hybrids usually have low stamen counts, and many of them are sterile, with the exception of one form, which has up to 60 stamens, they have 20 to 29, rarely up to 40 stamens. The species with the hirsutus type of inflorescences have the lowest stamen count, ranging 13 to 33. Such a general pattern when correlated with the form of buds, the type of inflorescences and the shape of fruits and the tails of the seeds, may serve as auxiliary criteria for characterizing sections or series of the genus.

Hitchcock was the first person who observed the tendency of the union of the lower portions of the filaments of several adjacent stamens into bundles in *P. argenteus* Rydb. (Pl. IV, fig. 8c), and used this character for distinguishing that xerophytic taxon. Normally the filaments of *Philadelphus* are separated. They are always shorter than the petals. With the exception of the extreme xerophytic dwarf forms like *P. serpyllifolius* Gray or *P. mearnsii* Evans, which has very small flowers and



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short stamens, the length of the filaments in *Philadelphus* is rather constant, with the longest outermost ones being 6–9 mm. long and that of the shortest innermost ones 2–3 mm. long. In the xerophytic forms, the filament of the outer stamens measures up to 4 mm. long and the inner ones 2 mm. long. So far as I know, the longest filament of *Philadelphus* is found in a garden form called *P. "slavini"* hort ex Wymn. with the inner filaments 7 mm. and the outer ones 12 mm. long. The filaments of *Philadelphus* have not and very likely never will furnish outstanding characters for distinguishing taxa of any rank in the classification of the genus.

The anthers of *Philadelphus* are generally oblong, being 1–1.2 mm. long, 0.9 mm. wide. The xerophytic species like *P. serpyllifolius* Gray has subglobose anthers, 0.5 mm. in diameter. There are a few natural populations occurring in Central China and western North America where hair-like processes occur on the thecae of the anthers (Pl. IV, fig. 8c). This is probably an expression of an unusual mutation which eventually may lead to speciation.

Pistil: A normal pistil of *Philadelphus* is composed of four carpels. Occasionally few 5-carpelled or very rarely some 3-carpelled pistils may occur in a garden form. Characters furnished by the parts of the pistil, ovary, style, and stigmas, have been employed for distinguishing taxa of various rank in *Philadelphus*. Schrader recognized *P. speciosus* for its 8-loculed fruit. Pursh distinguished his *P. lewisii* for its relatively long and much divided style. Koehne subdivided the major groups of the genus on the basis of the size of the stigma. Ruprecht, Koehne and many others have proposed species because of the presence of hairs on the style, or disc, or both. Nevertheless, due to our limited knowledge of the pistil in *Philadelphus* unnecessary binomials have been created. A normal *Philadelphus* ovary has four locules and an axile placentation. In each locule there are a pair of more or less fused auricular placentas projecting from the upper portion of the central column (Pl. I, fig. 10–12). The superior lobes of these placentas are much shorter than the inferior ones, the latter are so pressed together that they appear as one organ in cross sections (Pl. I, fig. 10B). In *P. inodorus* Linn., its varieties, and its related species, the inner wall of the roof of each locule, which corresponds

PLATE III

FLOWERS OF *PHILADELPHUS* CULTIVATED IN THE ARNOLD ARBORETUM SHOWING DIFFERENT FORMS OF THE COROLLA, THE READING IS BY THE COLUMNS 1, 2, 3, AND 4, EACH FROM THE TOP TO THE BOTTOM:

COLUMN 1. *P. "Argentine," P. grandiflorus, P. caucasicus, P. coronarius "speciosissimus," P. coronarius, var. primulaeflorus, P. coronarius*; COLUMN 2. *P. insignis (?) , P. incanus, P. falconeri, P. floridus, P. delavayi, P. "Cole Glorious"*; COLUMN 3. *P. "Belle Etoile," P. satsumanus, P. lemoinei, P. laxus, P. magdalenae, P. splendens*; COLUMN 4. *P. maximus, P. sericanthus, P. tenuifolius, P. pekinensis, P. nepalensis, P. "bicolor"*; COLUMN 5. *P. "Favorite," P. virginialis, P. "Norma," P. zeyheri, P. tomentosus, P. purpurascens.*

to the upper portion of the middle of the carpel, grows down and projects between the superior lobes of the placentas in such a manner that it appears like a false septum separating those lobes. Thus the cross sections made through the upper portion of a normal 4-locular ovary of such species appear 8-chambered (Pl. I, fig. 10D). This was perhaps what Schrader saw in *P. speciosus*. The position of the attachment of the placentas on the central column affects the shape of the fruit and the length of the tail of the seed. In *P. inodorus* Linn. the placentas are attached above the insertion of the sepals. Consequently the fruits are ellipsoid with circumferential sepals. These fruits have long-tailed seeds (Pl. I, fig. 10). On the other hand, the placentas of *P. microphyllus* Gray are attached about the same level as the insertion of the sepals (Pl. I, fig. 11). The fruits are ellipsoid with supermedian persistent sepals, and the seeds are short-tailed. In *P. hirsutus* Nutt. the placentas are attached below the insertion of the sepals (Pl. I, fig. 12). The fruits are obconic with apical persistent sepals and the seeds are ecaudate. This correlation of the attachment of the placentation, the shape of the fruits and the length of the tails of the seeds indicate that the position of the placentas can be used as auxiliary criteria for the delimitation of subgenera or sections of *Philadelphus*.

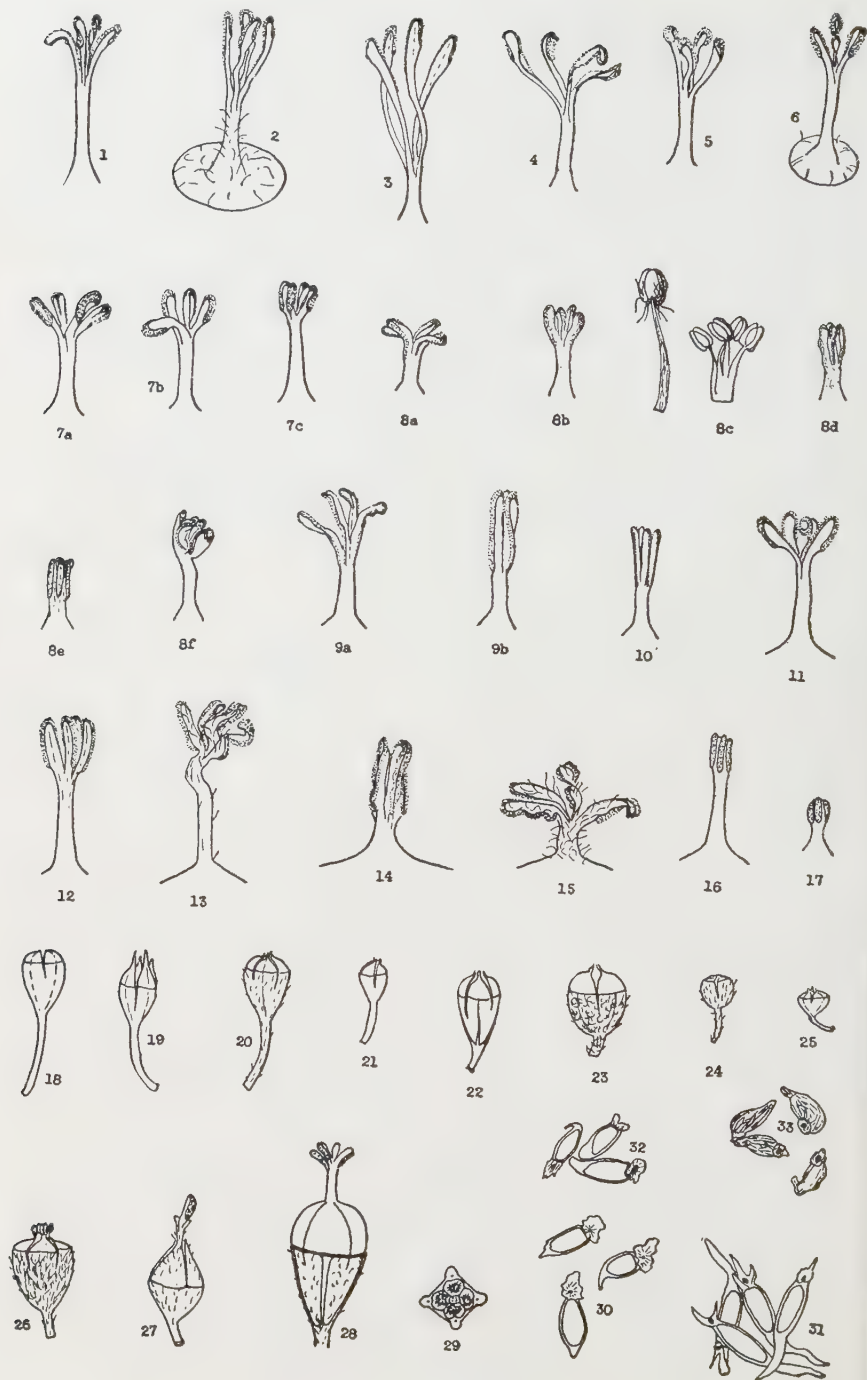
The length and the degree of the union of the style, the number and shape of the stigma and the indumentum of the style and disc have all been used in the classification of *Philadelphus*. Michaux in 1803 in distinguishing *P. inodorus* Linn. from *P. coronarius* Linn. introduced the relative length of the style and the stamens and the degree of union of the style. Since then Pursh has characterized *P. lewisii* as a species with three stigmas and a 3-parted style as long as the stamens, and Nuttall has characterized his *P. hirsutus* as a species with clavate undivided 4-grooved stigma and a style shorter than the stamens. Fortunately the species that Michaux, Pursh and Nuttall dealt with each represents a phylogenetically unrelated group, and incidentally the character holds true for distinguishing them. Later authors including Rydberg and Rehder have used the same character for delimiting closely related species, varieties and garden forms which present varied degrees related union of the styles. *Philadelphus microphyllus* Gray has been treated as a species with united stigma. But flowers of different collections exhibit varied degree of the union of the styles. Some are completely united, some are partially united and others are completely separated (Pl. IV, fig. 8a, b, e, f). This happens also in *P. argyrocalyx* Wooton (Pl. IV, fig. 9 A-b). So far as I know there is a variation in the degree of the union of the style in every natural population. For this reason such characters fail to be of value for distinguishing species or taxa of lower rank.

There are certain morphological differences existing in the styles and stigmas of geographically separated groups, which, when correlated with characters as the position of buds and the type of inflorescences, may be used as auxiliary criteria for demarcating series or sections. The styles of the southern Mexican species may be long or short, but they all have

elongated cristate stigmas with the fertile papillose surfaces situated largely on the elevated abaxial sides (Pl. IV, fig. 13-15). The styles of the southern Appalachian species with pauciflorous inflorescences are relatively long. They carry oar-shaped stigmas with adaxial as well as abaxial fertile papillose surfaces, the latter though definite in outline, are shorter (Pl. IV, fig. 12). The styles of the Old and the New World species with determinate-racemose inflorescences are comparatively long with clavate or linear stigmas. The fertile surfaces of these stigmas, with the exception of some Yunnan and Japanese species, are longer on the adaxial sides than on the abaxial sides (Pl. IV, fig. 1-6). The styles of the New World xerophytic species with pauciflorous inflorescences are relatively short with linear stigmas, the fertile surfaces of which are largely on the abaxial sides (Pl. IV, fig. 8-9). The styles of the New World species with the hirsutus type of inflorescences are columnar with subcapitate 4-grooved stigmas (Pl. IV, fig. 16-17).

The presence or absence of hairs on the disc and style is a definite and easily recognizable character which may safely be used in the identification of species. Ruprecht in 1857 first used such a character for *P. schrenkii*. Koehne later described *P. lancifolius* from Sikkim, *P. karwinskyanus* from Mexico, *P. subcanus* from Central China and *P. caucasicus* from western Asia on the strength of the same character. Rydberg in 1905 employed this character as the principal criterion in his key. But as abundant material is available for a comparative study of the natural populations of various regions this character is probably not as important as earlier taxonomists considered it to be. In nature among closely related taxa in all regions, there are paired species which differ chiefly in the absence or presence of hairs on the style, disc or both. For example, there are the *P. coronarius* and *P. caucasicus* in southern Europe and western Asia, *P. tenuifolius* and *P. schrenkii* in northeastern Asia, *P. subcanus* and *P. incanus* in Central China, *P. satzumi* and *P. lasiogynus* in Japan, *P. lewisii* and *P. gordonianus* in northwestern United States, *P. stramineus* and *P. pumilus* in southwestern United States, *P. pubescens*, and *P. gattlingii* in southeastern United States, and *P. coulteri* and *P. asperifolius* in Mexico. It is not impossible that such phenomena merely represent an expression of normal Mendelian inheritance of one character. But our knowledge of the genetics of these groups is lacking. For the present, and in the absence of cytogenetic information, the presence or absence of hairs on the disc, style, or both is retained for the purpose of distinguishing certain manifestly closely related taxa.

Capsules: The fruit of *Philadelphus* has not been used to any extent in the classification of its various taxa. The material that I have examined apparently presents subgeneric or at least sectional differences in the shape of the capsules and the position of their persistent sepals. The southeastern Mexican species all possess ellipsoid or obovoid fruits with median sepals while the northeastern Mexican species have globose fruits and subapical sepals (Pl. IV, fig. 26-28). The pauciflorous species have ellipsoid fruits and median persistent sepals while the species of the same



HU, THE GENUS *PHILADELPHUS*

area possessing the hirsutus type of inflorescences have obconic fruits with apical persistent sepals (Pl. IV, fig. 25). The position of the persistent sepals may be used as a satisfactory auxiliary criterion in distinguishing morphologically close but geographically remote species. *Philadelphus lewisii* Pursh and *P. pekinensis* Rupr. both have pseudoracemose inflorescences and glabrous hypanthia. Besides the geographical separation, the subapical sepals attached to the fruit of the former and the apical ones

PLATE IV

THE STYLE AND STIGMA OF *Philadelphus* (all $\times 2\frac{1}{2}$). 1. *P. coronarius*, the stigmas slightly enlarged, the abaxial surface definite, shorter than the adaxial. 2. *P. caucasicus* with pubescent style and disk. 3. *P. coronarius* var. *duplex* (Kew 1307); the stigmas broadened. 4. *P. tomentosus*, the adaxial surface split into two. 5. *P. pekinensis*, the abaxial surfaces much shorter than the adaxial. 6. *P. kansuensis*, the stigmas often 3, the disk with few hairs, the abaxial surface much longer than that of *P. pekinensis*. 7. *P. delavayi*, a. and c. from Yunnan (Feng 1012), b. from Latong, Tibet (Younghusband). 8. a-b and d-f. *P. microphyllus* with the styles separated in various degrees, the fertile surface of the stigma abaxial (a. Ellis 107, b. Eggleston 18654, d. Heller 3792 and f. Alexander-Kellogg 1785). 9. *P. argyrocalyx* with the stigmas separated or united (a. Eggleston 14541, b. Wootton in 1895). 10. *P. argenteus* with the style slightly separated (Mearns 1617). 11. *P. inodorus* with oar-shaped stigmas, the abaxial surfaces broadened, shorter than the narrow adaxial surfaces (AA15347). 12. *P. "bicolore"* with elongated style and enlarged stigmas (Hu in 1951). 13. *P. affinis*, the style long and hairy, the stigmas elongated with few hairs on the sterile portion (Berlandier 333). 14. *P. calcicolus* with the stigmas more or less united, broadened and cristate, the style short, glabrous (Meyer & Roger 2662). 15. *P. karwinskyanus* with the stigmas cristate and hairy on the sterile portion, the style short and pubescent. 16. *P. hirsutus* with the style comparatively long, the stigmas clavate and undivided, the stigmas on 4 ridges. 17. *P. serpyllifolius* with the style short, the stigmas undivided and subcapitate.

FRUIT OF *Philadelphus* ($\times 1$). 18. *P. tenuifolius* with the apical end rounded (Cen. 263). 19. *P. tomentosus* with the apical end pointed and the persistent calyx almost circumferential (Parker, in 1919). 20. *P. sericanthus* with the apical end rounded, the lower portion pubescent. (Steward, Chiao & Cheo 609). 21. *P. pekinensis* with very small fruit (King 626). 22. *P. inodorus* with ellipsoid fruit. 23. *P. argyrocalyx* with subglobose fruit, the lower portion lanate (Rehder 315). 24. *P. hirsutus* with flat apical end (Biltmore Herb. 4333). 25. *P. hitchcockianus* with very small top-shaped fruit which is broader than long (Moore 3477). 26. *P. sargentianus* with subglobose fruit (Pringle 2094). 27. *P. karwinskyanus* with ellipsoid fruit pointed at both ends (Rose & Hough 4412). 28. *P. mexicanus* with obovoid fruit the lower portion 4-angled. 29. Cross-section of the fruit of *P. mexicanus*, one third from the base.

SEEDS OF *Philadelphus* ($\times 10$). 30. The short-caudate seed of *P. pekinensis* with round-lobed crown. 31. The long-caudate seed of *P. inodorus* with pointed-lobed crown. 32. The short-caudate seed of *P. californicus*. 33. The ecaudate seed of *P. hirsutus*.

SOME UNUSUAL STAMENS OF *Philadelphus*. 8c. Stamens with fused filaments (Eggleston 18654). 8g. Stamen with hirtellous anther (Abram 7200).

to the fruit of the latter are outstanding characters for distinguishing these species.

Seeds: Seeds are minute in all species of *Philadelphus*. Each individual seed consists of a small ellipsoid body about 1–2 mm. long wrapped in a thin testa extending towards both ends. The large portion of this small body is the copious oily endosperm which imbeds the microscopic embryo. The hypocotyl and the radicle constitute two-thirds of the embryo proper. The cotyledons and the epicotyl are very minute. The testa is reticulate, light brown, castaneous, or rarely black. It extends into an irregular collar-like crown at the proximal end and a tail-like wing at the distal end. The crowns of the seeds of different species vary in shape. That of the seed of *P. pekinensis* Rupr. has more or less rounded lobes (Pl. IV, fig. 30), that of the seed of *P. inodorus* Linn. has pointed lobes (Pl. IV, fig. 31), and that of the seed of *P. hirsutus* Nutt. is very minute and inconspicuous (Pl. IV, fig. 33). The length of the seed-tail varies as well as the shape of the crown. *Philadelphus inodorus* Linn. has a long-tailed seed, *P. pekinensis* Rupr. has a short-tailed seed and the seed of *P. hirsutus* Nutt. has no tail. Seed characters have never been used in the classification of *Philadelphus*. The shape of the crown and the length of the tail of the seed correlate with the position of the buds, the type of the inflorescence, and the form of the stigma. In my opinion they are characters of subgeneric or sectional importance. In some cases they can be used to distinguish intricate species. For example, because of the superficial similarities of the leaves and the corollas of *P. lewisii* Pursh and *P. californicus* Benth. and also because of their overlapping geographic distribution, some botanists have placed the latter as a variety of the former. As *P. lewisii* Pursh has long-tailed seeds and *P. californicus* Benth. has short-tailed seeds (Pl. IV, fig. 32), and as this character is associated with the difference in the inflorescences, *P. californicus* Benth. should be considered as a good species.

In summarizing the study of the gross morphology of *Philadelphus*, it seems legitimate to conclude that characters such as the dichasial inflorescence, large number of stamens, elongated stigma with enlarged papillose fertile surface, high insertion point in the placentation, ellipsoid fruit with circumferential calyx lobes, and long-tailed seed can be interpreted as primitive ones, while in contrast, characters like solitary flower, the racemose or paniculate inflorescence, the small number of stamens, the reduced length of the stigma, the low point of insertion in the placentation, the obconic fruit with apical persistent sepals and the short-tailed seed can be interpreted as representing more advance stages in the evolution of the genus.

SUBDIVISIONS OF THE GENUS AND THE PHYLOGENY OF ITS MAJOR GROUPS

Based on the data found in the position of the buds, in the type of inflorescences, in the form of stigmas, in the shape and position of the persistent sepals on the fruits, and the nature of the seeds, I am arranging

the species of *Philadelphus* into four subgenera and nine sections. The characters of these taxa are stated in the following synopsis.

SUBGENUS I. *Gemmatus*: This subgenus includes all the species with exposed buds; depauperate paniculate inflorescences, one or three terminal flowers with jointed pedicels or many flowers in ramified branchlets; stamens 40–60; semi-inferior ovary, enlarged and often cristate, separated stigmas; obovoid-ellipsoid or subglobose fruits with circumferential sepals; and long-caudate seeds. It contains 14 species in two sections.

SECTION 1. *Poecilostigma*: Inflorescences compound, 1- up to many-flowered; stamens 40 to 50; stigmas elongated and cristate; fruits obovoid-ellipsoid; southeastern Mexico, Guatemala to Costa Rica.

SECTION 2. *Coulterianus*: Inflorescences with solitary flowers, rarely 3-flowered; stamens 30–44; stigmas elongate, not cristate; fruit subglobose; northeastern Mexico.

SUBGENUS II. *Euphiladelphus*: This subgenus includes all the species with enclosed buds, determined branches, determinate-racemose or pauciflorous inflorescences, large or medium number of stamens, clavate or oar-shaped or linear stigmas, and long- or short-tailed seeds. It comprises 41 species in three sections.

SECTION 3. *Pauciflorus*: Inflorescences true dichasial cymes, often reduced to one or three flowers; stamens 60–90; stigmas oar-shaped; fruit ellipsoid with circumferential sepals; seeds long-tailed with pointed lobes on the crown; two species, native of the Southern Appalachian region of the United States.

SECTION 4. *Stenostigma*: Inflorescences determinate-racemose; stamens 25–35, rarely over 40; stigmas clavate or linear; fruit ellipsoid with subapical persistent sepals; seeds long- or short-tailed, the crown with pointed or rounded lobes; 30 species in both the Old and the New Worlds.

SECTION 5. *Microphyllus*: Inflorescences pauciflorous; stamens 25–40, rarely up to 50, stigmas linear; fruit ellipsoid with circumferential or subapical persistent sepals; seeds short-tailed with rounded lobes on the crown; 11 species, Colorado Plateau, Mexican Highland, and northern Mexico.

SUBGENUS III. *Marcrothyrsus*: This subgenus includes species with exposed buds; determined branches, paniculate inflorescences; medium number of stamens; clavate stigmas, and short-tailed seeds. It has one section including three species, native of California.

SECTION 6. *Californicus*: Characters as the subgenus.

SUBGENUS IV. *Deutzioides*: This subgenus includes all the species with exposed buds, and indeterminate branches; solitary, rarely ternate flowers; 13–35 stamens; inferior ovary, and columnar or subcapitate 4-grooved stigmas; turbinate or subglobose fruits with apical persistent sepals, and ecaudate seeds. It comprises eight species in three sections.

SECTION 7. *Hirsutus*: Flowers ternate; mesophytic plants; leaves serrate, hirsute, hairs all straight, style 4 mm. long; two species, Tennessee, Alabama.

SECTION 8. *Pseudoserpyllifolius*: Flowers solitary; xerophytic, dwarf plants, leaves entire, strigose or strigose-villose, hairs all straight; style up to 1 mm. long; four species, Texas, New Mexico, and Northern Mexico.

SECTION 9. *Serpyllifolius*: Flowers solitary; xerophytic, dwarf plants, leaves entire, lanate and hirsute beneath, trichomes dimorphous; two species, Texas, New Mexico, Arizona, Northern Mexico.

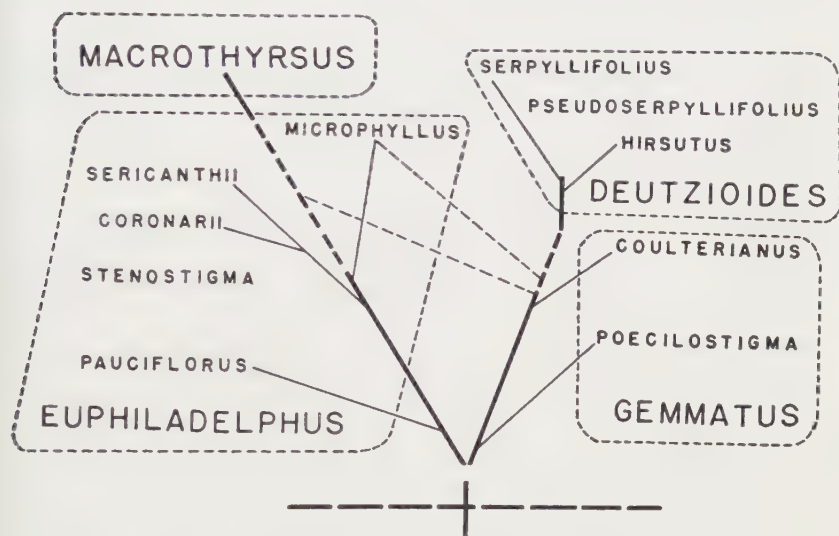
The interrelationship of the subgenera and sections is indicated graphically in the following figure.

In this classification primitive characters such as enlarged stigmas, high point of attachment in the placentation and long-tailed seeds are found both in the section *Pauciflorus* of the subgenus *Euphiladelphus* and the section *Poecilostigma* of the subgenus *Gemmatus*. The true dichasial inflorescences and the very large number of stamens of sect. *Pauciflorus* indicate that species in this section retain more primitive characters than those of sect. *Poecilostigma* which has apparently reduced compound inflorescences and moderate number of stamens. Yet the exposed buds of sect. *Poecilostigma* and the elongated cristate stigmas of many of its included species show that this section is more primitive in these respects. Morphological evidences, obviously suggest that our present species of *Philadelphus* seem to express two lines of evolution. They probably have originated from a common stock with exposed buds, dichasial inflorescences, exceedingly large number of stamens, and elongated cristate stigmas. Such a hypothetical "*Protophiladelphus*" does not exist in our present flora. The species of the section *Pauciflorus* occur in the mesophyllous forest of the southern Appalachian region, and those of the section *Poecilostigma* are associated with vegetations constituting the same type of forest in Mexico.¹ Apparently species in these two sections have existed for millions of years with very little changes.² They both represent very ancient stocks in the development of the genus.

¹ A. J. SHARP, Characteristics of the Vegetation in Certain Temperate Regions of Eastern Mexico. *Ecology* 31: 313–333. 1950.

² S. A. CAIN, The Tertiary Character of the Cove Hardwood Forests of the Great Smoky Mountains National Park. *Bull. of the Torrey Bot. Club* 70: 213–235. 1943; and A. J. SHARP, The relation of the Eocene Wilcox Flora to some Modern Floras. *Evolution* 5: 1–5. 1951.

Species of the sect. *Stenostigma* share the character of enclosed buds with the sect. *Pauciflorus*. This section with its determinate-racemose inflorescences, moderate number of stamens and some long-tailed but largely short-tailed seeds seems to have derived from the sect. *Pauciflorus*, the direct link seems to be from the *P. inodorus* type of plant to the *P. lewisii* type of plant. In this process of evolution, the changes involved are: (1) the suppression of the branching of the rachis of the lateral flowers of the true dichasia of the sect. *Pauciflorus*, thus prohibiting the formation of



HYPOTHETICAL PROTOPHILADELPHUS

FIG. 1. Relationships of the subgenera and sections of *Philadelphus* as indicated by morphological similarities. The solid lines indicate relative close relationships while the broken lines indicate lesser affinities.

the lateral cymes, (2) certain genetic modifications which promotes the differentiation of the tissue in the shoot apex, so that flower primordia are formed not only at the terminal nodes, but also in the axils of the leaf primordia, and consequently the determinate-inflorescences of the sect. *Stenostigma* are developed, (3) the reduction of the number of stamens, (4) the narrowing of the stigmatic surfaces, and (5) the lowering of the point of attachment in the placentation. The shortening of the seed-tails represents a more advanced stage of evolution in this section. These changes must have taken place before the Miocene period of geological time for fossil species of *Philadelphus* resembling the present small-leaved forms of *P. lewisii* Pursh existing in the Upper Miocene have been discovered by Chaney in Oregon and Colorado. It is very probable that during the Eocene period when North America, northern Asia and north-

ern Europe supported a temperate and subtropic flora, the species of the section *Stenostigma* were so well established and so widely distributed on the American and Eurasian continents that they had a holarctic distribution and a transcontinental range. The present disjuncted Old World and New World distribution represents its disturbed range and the existing species of this section may hence be considered as "living fossils" corresponding to the situation of *Sequoia* and *Metasequoia*.

The section *Microphyllus* culminates the *Euphiladelphus* line of descent. Its species share the characters of narrow stigmas and short-tailed seeds with the section *Stenostigma*. The majority of them have small leaves and pubescent hypanthia, characters common to xerophytic species. In the course of the evolution of these species the changes involved are chiefly in the development of the dwarf habit of the plant, in the reduction of the size and the increase in the thickness of the leaves, the formation of dense indumentum and in the suppression of the formation of the axillary flowers. These changes must have taken place at or after the end of the Eocene period when America saw the elevation of the Rocky Mountains. The consequent aridity necessitated such adaptation for xerophytic living.

The subgenus *Macrothyrsus*, though small in constitution, has a peculiar position in the classification and evolution of *Philadelphus*. On one hand it shares the moderate number of stamens, the clavate stigmas, the medianly attached placentation and the short-tailed seeds with species in the *Stenostigma* section of the subgenus *Euphiladelphus* but on the other hand its exposed buds link it to the subgenus *Gemmatus*. In addition to this peculiar combination of characters its paniculate inflorescence is very unique. It is probably most closely related to the subgenus *Euphiladelphus*. The general habit, the leaves and the appearance of the individual flowers of its included species, *P. californicus* Benth., resemble those of *P. lewisii* Pursh, a species of the section *Stenostigma* of the *Euphiladelphus*, so much that it has tempted botanists to treat it as a variety of the latter species. Apparently this stock has originated from the subgenus *Euphiladelphus* with a tenuous influence of the section *Gemmatus*.

The species of the section *Coulterianus* share the exposed buds and the long-tailed seeds with the *Poecilostigma*. Apparently this section represents a continuation of the *Gemmatus* line of evolution. In this stock a general tendency in the adaptation for a more xerophytic habitat is very prominent. It is shown both in the reduction of the size of the leaves and in the increased thickness of the indumentum. The stigmas of this section are elongate but not as a rule cristate, and the fruits are more or less globose in outline. In the size of the leaves, the pubescences of the hypanthia and in the form of the fruits, some species of this section, such as *P. sargentianus* S. Y. Hu express a strong resemblance to *P. argyrocalyx* Wootton of the section *Microphyllus* of the subgenus *Euphiladelphus*. These similarities are rather superficial. The gap between these species is wide for they differ in the fundamental criteria as to the position of the buds and the nature of the seeds.

Morphologically the subgenus *Deutzioides* is only remotely related to *Philadelphus*. In the low point of attachment of the placentation, the obconic fruit and the tailless seeds, this subgenus shows a close affinity to the Asiatic genus *Deutzia*. In fact, the appearance of a branch of *P. hirsutus* Nutt., the type species of the section *Hirsutus*, resembles that of a branch of *Deutzia grandiflora* Bge. of West China (Szechuan and Yunnan) more than it does of any American species of *Philadelphus*. Nevertheless, the species of this subgenus should not be separated from *Philadelphus* because of the indefinite number of unappendaged stamens and the simple straight hairs. In *Deutzia* the stamens are usually 10 and are always appendaged, that is, the filaments are winged. The trichomes of *Deutzia* are all stellate. The point of origin of this line of evolution in *Philadelphus* is not clear, but evidently it was not from the stock which gave rise to the *Euphiladelphus* species. The exposed buds of this subgenus indicate its faint affinity with the subgenus *Gemmatus*. Yet its ecaudate seeds, the columnar styles, and the coalescent stigmas imply a wide gap between them. It seems apparent that in the course of the evolution of *Philadelphus*, there has been a tendency towards the production of *Deutzia*-like plants. It appears that in the New World the process stopped in the subgenus *Deutzioides*, while in the Old World the change was more abrupt, the resulting genus, *Deutzia*, once established, diversified more rapidly than *Philadelphus*, and consequently occupies a wider area than *Philadelphus*. This conforms with Professor Sax's finding in the chromosome numbers of the two genera.¹ Accordingly, the basic chromosome number of *Philadelphus* and *Deutzia* are the same, $n = 13$, but in *Deutzia*, many species are polyploids. The xerophytic taxa of the subgenus *Deutzioides* may have the appearance of some species of the section *Microphyllus*. For example, *P. mearnsii* Evans of the section *Pseudoserpyllifolius* resembles *P. pumilus* Rydb., and *P. texensis* S. Y. Hu of the section *Serpyllifolius* has the appearance of *P. microphyllus* Gray. But these resemblances are superficial. *Philadelphus mearnsii* and *P. serpyllifolius* have exposed axillary buds, columnar styles, and ecaudate seeds and *P. pumilus* and *P. microphyllus* have enclosed buds, divided styles and short-tailed seeds. These superficially resembled species are developed from different stocks, the separation of which occurred in remote geological times. The exposed buds and the large serrate leaves of *P. hirsutus* Nutt. resemble those of *P. mexicanus* Schlecht. But the low point of attachment in the placentation, the columnar style and the ecaudate seeds of the former species indicate its advanced position on the genealogical tree of the genus. It is legitimate to assume that the representatives of the section *Hirsutus* were derived from the subgenus *Gemmatus* early in the evolution of the genus, and developed independently into the present forms. The species of the section *Pseudoserpyllifolius* are pygmies of this line of development and come about through the reduction in the size of the leaf to meet changed climatic and topographic require-

¹ K. SAX, Chromosome numbers in the Ligneous Saxifragaceae. Jour. Arnold Arb. 12: 198-204, 1931.

ments characteristic of a xerophytic environment. They are intermediate forms between members of the sections *Hirsutus* and *Serpyllifolius*. In indumentum they resemble the former and in size and general appearance they resemble the latter. The species of the section *Serpyllifolius* represent the climax of this line of evolution.

CYTOLOGY

Investigations of the cytology of *Philadelphus* have been undertaken by W. Bangham in Boston and Janaki Ammal in London. Bangham in 1929¹ examined the pollen mother cells of 37 species, hybrids and varieties of *Philadelphus* grown in the Arnold Arboretum and concluded that there is no marked difference in the chromosome groups among those taxa. He reported that each species had a diploid chromosome count of 26. He observed that the chromosomes of the hybrids were perfectly compatible and there was no evidence of lagging and other aberrant behavior. His observation on the chromosome behavior of a garden form of *P. pubescens* Loisel., which was then assumed by Rehder to be a cross between *P. tomentosus* Wall. of the Himalayan Region and *P. pubescens* Loisel. of southeastern United States, led him to conclude that there must have been very little change in the chromosome makeup of *P. tomentosus* Wall. and *P. pubescens* Loisel. in the millions of years that they, or their ancestors, have been separated.

Janaki Ammal in 1951² studied the chromosome number and behavior of *Philadelphus* grown at the Royal Botanic Gardens, Kew and the gardens of the Royal Horticultural Society at Wisley, England. She confirmed Bangham's findings that the natural species are diploids with the chromosomes $2n = 26$. But her observation of the chromosome behavior of the hybrids differs from that of Bangham. She reported that lagging and other types of aberrant behavior are generally associated with hybridity in *Philadelphus* and consequently give rise to high pollen sterility. In the case of the trispecific hybrids, *P. purpureo-maculatus* Rehd., the chromosome behavior is so irregular that it causes the production of unreduced germ cells. By the fertilization of an unreduced egg cell with a normal pollen, triploid garden forms resulted. She found that *P. "Sybille,"* *P. "Belle Etoile"* and *P. "bicolor"* are all triploids. She also observed a newly produced hybrid, *P. "Beauclerk,"* with tetrasomic diploid chromosome composition, $2n = 28$. She thus concluded, "though differences in chromosome number do not exist in nature, there are differences in morphology of the chromosome which interfere with pairing in their hybrids between widely separated species . . . for the first time since Eocene times polyploidy has been induced in a genus which has remained diploid for millions of years in nature, by the bringing together under cultivation

¹ The Chromosomes of Some Species of the Genus *Philadelphus*. Jour. Arnold Arb. 10: 167-169. 1929.

² Chromosomes and the evolution of Garden *Philadelphus*. Jour. Royal Hort. Soc. 76(8): 269-275. 1951.

and the consequent hybridization of races widely separated geographically."

Bangham worked on plants cultivated in Boston and Janaki Ammal's material was grown in London. These two cities are located out of the natural ranges of the genus *Philadelphus*. The climate of these cities only supports the outdoor growth of a few species and their forms. A close examination of the lists of species studied by Bangham and Janaki Ammal reveals that they covered very limited portions of the geographically widely spread and morphologically much diversified genus. Thus it appears to me that the cytological investigation of the natural species is not inclusive enough for any cytologist to draw a conclusion as to whether differences in the chromosome number of *Philadelphus* do exist in nature or not. A large scale transplanting of natural species from southeastern and western United States and Central America into gardens situated in areas warmer than Boston or London, such as the United States National Arboretum in Washington, D. C. or the Boyce Thompson Southwestern Arboretum for the study of the drought resisting species, will doubtlessly provide better opportunities for more exhaustive cytological studies of the genus and advance our knowledge of the cytotaxonomy in this group.

GEOGRAPHIC DISTRIBUTION

The subgenus *Gemmatus* with its exposed axillary buds, simple, reduced or ramiferous thyrses, high point of attachment in the placenta, broadened usually cristate stigma and long-tailed seeds, represents morphologically, I feel, the more primitive elements of the genus. The species are largely subtropical or tropical in distribution. They are limited to the New World, with eastern Mexico being its center of concentration. The range extends ten degrees toward the north and the south of the Tropic of Cancer. The effect of rainfall, temperature, altitude and latitude on the distribution of the different species of this subgenus in Mexico is very evident. *Philadelphus karwinskyanus* is found only on the Great Cross Range and hence westward along the Pacific Coast at lower altitudes where the climate is warmer. In the warm and humid section of the Sierra Madre Oriental, one finds *P. affinis* with its subglabrous hypanthium. At higher altitudes of the same range grows the small-flowered *P. asperifolius*. Hence northward into the arid northeastern Mexico, occur various endemic species belonging to the Section *Coulterianus*. In the neighborhood of the Tropic of Cancer at high altitude where the rainfall is low, *P. maculatus*, a small-leaved form with reddish purple spot at the base of each petal, grows.

The true *P. mexicanus* with its solitary or ternate flowers and pubescent petals occurs only on the Sierra Madre del Sur, the southern area of the Sierra Madre Oriental, and in Chiapas, hence southwestward to Guatemala. In southern Mexico and Guatemala, a species with pubescent petals and ramiferous inflorescences, *P. myrtoides*, occurs. This species extends southward to the Province of Chiriqui in Panama, the southern limit of the range of distribution in the genus.

The subgenus *Euphiladelphus* includes geographically the more widely distributed elements. Its representatives occur in Europe, Caucasus, the Himalayan region, China Proper, Manchuria, Japan, a large part of the United States, and adjacent southwestern Canada and northeastern Mexico. It is an assemblage of species adapted to the climatic conditions of the North Temperate Zone, between latitudes 25–50° N. in both the Old and the New World.

In the Old World, the subgenus is rather stable. Radical changes did not occur in the course of its evolution. All the Old World species belong to one section, *Stenostigma*. In Europe, it is represented by *P. coronarius* which occurs, according to Hegi, spontaneously in Romania, Austria and southern Germany. In the Caucasus Mountains, it is represented by *P. caucasicus*, a species which differs from *P. coronarius* only in its pubescent discs and styles. The eastward distribution of the section is interrupted in Central Asia. No species is met with until it reaches the Himalayan Mountains. There the species concentrate in Sikkim, Nepal and eastern Punjab where it is represented by *P. tomentosus* and its related forms. In China more marked morphological changes were involved in the course of the evolution of this group. There the section can be subdivided into several series. The Tsingling Range seems to provide a central stage from where the different lines of evolution in the species can be traced. At the western end of this mountain range occurs *P. kansuensis*, a species having the leaf character of *P. pekinensis*, a North China element, the pubescent disc of *P. subcanus*, a Central China element and the pubescent hypanthium of *P. henryi*, a southwestern China element. At the eastern end of this mountain range, occurs *P. sericanthus* and its related forms. South of this range grows *P. purpurascens*, an intermediate form between the Tsingling and the Yunnan species, *P. delavayi*. The latter species morphologically and geographically links the Chinese and the Himalayan elements. North of the Tsingling Range in Shansi, Shensi and Kansu occurs *P. laxiflorus*, a species morphologically and geographically intermediate between *P. pekinensis* and *P. sericanthus*. The northernmost limit of the distribution of this section in the Old World is the wooded valley of the Amur River and its tributaries, the Sungari and Ussuri rivers in Manchuria, where it is represented by *P. tenuifolius* and *P. schrenkii*. These species also occur in Korea. In Japan this subgenus is represented by *P. satsumi* and its related forms.

The distribution of *Philadelphus* in Eastern Asia presents a very interesting phytogeographic phenomenon, that is, the complete absence of the genus from the flora of Taiwan (Formosa). It is a well known fact that Taiwan and Yunnan have very pronounced floristic affinities. Many species as well as genera that occur in one province are also present in the other. But in the case of *Philadelphus*, the genus is abundant in northwestern Yunnan and is completely absent from Taiwan. This fact may be taken as an indicative factor for confirming our belief as to the origin of the genus and for explaining the pattern of its distribution in Eastern Asia. The genera and species that are common to Taiwan and

Yunnan are of Old World origin. *Philadelphus* is obviously of New World origin, and its distribution in Eastern Asia seems to have been southward in direction. Apparently neither the Japanese elements nor the continental Chinese elements of this genus reached Taiwan in their migration.

In the New World, the subgenus *Euphiladelphus* is much more diversified, and consequently three sections are represented. Two of these three sections, *Pauciflorus* and *Microphyllus*, are endemic to the United States. Few species of the section *Microphyllus* also occur at the northern border of Mexico. The third section, *Stenostigma*, America shares with Europe and Asia. In North America the species of the section *Stenostigma* can be subdivided into two series the *Gordoniani* and the *Pubescentes*. Species belonging to the *Gordoniani* series occur along the Snake and Columbia Rivers, hence southward reaching the mountains of the California Coast Range. Among the wild population, there seems to be two elements, *P. lewisii* with a glabrous hypanthium and *P. helleri* with a slightly pubescent hypanthium. Morphologically there seems to be little distinction between them, other than the presence or absence of the hairs on the hypanthium, but ecologically there are certain differences. In the natural population of the general area considered, I have examined 292 individual collections totaling 361 sheets. Of these, 177 have glabrous hypanthia and 115 have slightly pubescent ones. After plotting the localities of these collections on a map and then superposing this figure on Rehder's map of climatic zones,¹ a rather striking fact is revealed. Over 77% of *P. lewisii* occur in zones where the average annual minimum temperature is -10° to -5° F. while over 47% of *P. helleri* occur in zones where the average annual minimum temperature falls to -20° to 10° F. The checking also indicates that the center of distribution of *P. lewisii* is in the lower valley of the Columbia River and in the northern portion of the Pacific Border Province while *P. helleri* occurs largely in the intermontane basin and the deeply dissected mountain uplands of the northern Rocky Mountains. Species belonging to the series *Pubescentes* occur in the Ozark Plateau and the Arkansas Valley of the Interior Highlands and the Interior Low Plateau region of Tennessee, Kentucky, and southern Ohio.

The section *Pauciflorus* with dichasial inflorescences, very large number of stamens, enlarged stigmas, and high point of attachment in the placentation and long-tailed seeds, retains all the primitive characters of the genus. Species of this section concentrate in the mesophyllous forest of the southern Appalachian region with the periphery of their range reaching the Coastal Plain region along the borders of Georgia and Alabama in the south. It seems that species of this section are rather inactive geographically and stable morphologically, for with all the material I have examined, there are very slight variations.

The section *Microphyllus* includes the xerophytic species. Its range covers the southern Rocky Mountains in Central Colorado, the Colorado Plateau in western Colorado, Utah, northern New Mexico and Northern Arizona, the Sonoran Desert region in southern Nevada and southeastern

¹ Man. Cult. Trees, Shrubs pp. xii-xiii, 1940.

California and the Mexican Highland in Eastern Arizona, southwestern New Mexico and western Texas, and the adjoining Mexico. In this large semidesert or desert area the populations are localized and isolated. There are many endemics.

The subgenus *Deutzioides* is strictly a North American taxon. Its three sections occur in two different floristic provinces. The section *Hirsutus*, as represented by *P. hirsutus* Nutt. and its related forms, concentrates in the mesophyllous forests of the Southern Appalachian Mountain areas with the Tennessee River and its tributaries being the center of its range. The other two sections, *Pseudoserpyllifolius* and *Serpyllifolius*, are constituted of xerophytic species which occur in southwestern Texas, New Mexico, southern Arizona, and northern Mexico. It seems that the Mexican Highland is a meeting ground of different elements, the subgenus *Euphiladelphus* from the north, *Deutzioides* from the east and *Gemmatus* from the south.

TAXONOMY

Philadelphus Linn. Sp. Pl. 470. 1753; et Gen. Pl. ed. 5, 211. no. 540. 1754. — Miller, Dict. Gard. ed. 8, 834. 1768. — Willd. Sp. Pl. 2: 947. 1800. — Michx. Fl. Bor. Am. 1: 283. 1803. — Pursh, Fl. Am. Sept. 1: 329. 1814. — DC. Prodr. 3: 205. 1828. — Schrader in Linnaea 12: 388. 1838. — G. Don, Gen. Syst. 2: 807. 1832. — Schlecht. in Linnaea 13: 418. 1839. — Torr. & Gray, Fl. N. Am. 1: 594. 1840. — Endl. Gen. Pl. 1187. 1841. — Walp. Rep. 2: 151. 1843. — Koch in Woch. Gärtn. Pflanzenk. 2: 229. 1859. — Rupr. ex Maxim. in Bull. Phys.-Math. Acad. St. Pétersb. 15: 133. 1856; 15: 365. 1857. — Benth. & Hook. f., Gen. Pl. 1: 642. 1865. — Maxim. in Mém. Acad. Sci. St. Pétersb. VII. 10(16): 35 (Rev. Hydrang. As. Or.). 1867. — Koehne, Deutsche Dendr. 178. 1893; in Gartenfl. 45: 450. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 76. 1904. — Rydb. in N. Am. Fl. 22: 162. 1905. — Schneider, Ill. Handb. Laubh. 1: 1905. — Syreistchikof, Ill. Fl. Mosc. 2: 220. 1907. — Nakai in Bot. Mag. Tokyo 29: 61. 1915. — Moore in Bailey, Stand. Cycl. Hort. 5: 2579. 1916. — Rehd., Man. Cult. Trees Shrubs 270. 1927, ed. 2, 264. 1940; et Bibliogr. Cult. Trees Shrubs 191. 1949. — Engler, Pflanzenf. III, 2a: 69. fig. 36. A-G. 1891; ed. 2. 18a: 190. fig. 110. A-G. 1930. — Hitchcock in Madroño 7: 35. 1944. — Bean, Trees Shrubs ed. 7, 2: 410. 1950; et in Chitt. Dict. Gard. 3: 1545. 1951.

Syringa Adanson, Fam. Pl. 2: 244. 1763. — Moench, Meth. Pl. 678. 1794, non Linn. 1753.

TYPE SPECIES: *P. coronarius* Linn.

Flowers solitary, ternate, in determinate racemes or in depauperate panicles, generally fragrant. Calyx-tubes turbinate or subcampanulate, adnate to the ovary forming the hypanthia, glabrous or pubescent, the

sepals 4, rarely 5, ovate, acute or acuminate; corolla white, rarely with purplish center, the petals 4, rarely 5, in cultivated forms often doubled; stamens 13–90, epigynous, the filaments subulate, free, rarely several united at the base, the anthers oblong, rarely subglobose, glabrous, rarely pilose; ovary inferior or semi-inferior, 4-, rarely in anomalous forms 5-locular, the styles 4, rarely 3 or 5, entirely connate, partially free or rarely in some cultivated forms entirely free, the stigmas free and linear, clavate, oar-shaped, cristate, or coherent and columnar or subcapitate; placentas auriculate, projected from the upper portion of the central axis; ovules numerous, multiseriate, imbricate, pendulous. Capsules ellipsoid, turbinate, hemispherical or subglobose, corticate, the cortex chartaceous, the pericarp cartilaginous, loculicidal. Seeds oblong-subcylindric, the testa brown or nigrescent, membranous, reticulate, generally extending anteriorly into a fimbriate white crown and posteriorly into an obtuse or acuminate tail, the funiculus nigrescent, persistent, the embryo minute, embedded in the carnose and oily endosperm. Shrubs, erect, arching, subscandent or rarely subspinescent; branchlets opposite. Leaves opposite, deciduous, rarely evergreen, serrate or entire, triplinervate or quintuplinervate, glabrous or pubescent, the hairs simple, rarely evergreen, exstipulate; axillary buds exposed or enclosed.

The generic name, *Philadelphus*, is derived from the Greek root *φίλος* meaning love, *δελφός* meaning brother. It was originally used by the ancient Greeks, said to be named for Ptolemy Philadelphus, king of Egypt, 283–247 B. C., for some plant the identity of which is now unknown. Many pre-Linnaean authors called the plants which we now ascribe as *Philadelphus*, "*Syringa alba*." Clusius¹ named his illustration of the plant *Frutex coronarius*. Bauhin was the first man who interpreted the pre-Linnaean "*Syringa alba*" as the *Philadelphus* of the Greeks.² When Linnaeus established the genus, he adopted Bauhin's concept. The vernacular names occurring in various literatures are enumerated in the following list:

English:	<i>Syringa</i> ; common syringa; mock-oranges (for the odor of the flower); pipe tree; pipe privet
French:	<i>Syringa odorant</i>
German:	Pfeifenstrauch; wilder jasmin; falscher jasmin
Dutch:	Witte syring
Chinese:	T'ai-ping-hua = flower of peace; san-mei-hua = mountain mume flower; Mi-tsai = rice fuel.
Spanish:	Geringuilla
Russian:	Tschubuschnik; pustoryl
Central American:	Mosqueta; Acuilotl = water vine; cozticacuilotl; cozticacuilotl xochitl; azahar

¹ *Rariorum Plantarum Historia* 1: 55. 1601.

² *Pinax Theatri Botanici* 399. 1623.

KEY TO THE SUBGENERA AND SECTIONS.

- A. Axillary buds exposed.
- B. Seed long-caudate; stigmas free, broadened, usually cristate; flowers solitary, ternate, or in depauperate panicles; fruit obovoid or subglobose, with circumferential persistent calyx. . . . Subg. I. GEMMATUS.
- C. Leaves acuminate, rarely acute; flowers in a depauperate panicle, 1- up to many-flowered, each on a pointed pedicel; the stigmas broadened, cristate; fruits obovoid-ellipsoid Sect. 1. POECILOSTIGMA.
- CC. Leaves acute or obtuse; flowers solitary or ternate; the stigma elongate but in general not cristate; fruit subglobose Sect. 2. COULTERIANUS.
- BB. Seeds short-caudate; stigmas free, clavate; flowers in panicles of thyrsus; fruit ellipsoid with subapical persistent calyx. Subg. III. MACROTHYRSUS (Sect. 6 CALIFORNICUS)
- BBB. Seeds ecaudate; stigmas connate, columnar or subcapitate; flowers solitary or ternate; fruit turbinate or subglobose, with apical persistent calyx Subg. IV. DEUTZIOIDES.
- C. Leaves hirsute or strigose, all hairs straight.
- D. Style 3-4 mm. long; subsucculent shrubs; leaves serrate Sect. 7. HIRSUTUS.
- DD. Style 1 mm. long; subspinescent shrubs; leaves entire Sect. 8. PSEUDOSERPILLIFOLIUS.
- CC. Leaves strigose and lanate beneath; style 1-2 mm. long; subspinescent or small slender shrub Sect. 9. SERPYLLIFOLIUS.
- AA. Axillary buds enclosed Subg. II. EUPHILADELPHUS.
- B. Flowers solitary, ternate or in dichasial cymes.
- C. Large arching shrubs; stamens 60-90; stigmas free, oar-shaped; leaves 4-10 cm. long. Sect. 3. PAUCIFLORUS.
- CC. Erect low shrubs of compact growth or spinescent xerophytic bushes; stamens 35-50; stigmas free or partially connate, linear; leaves 0.5-2.5, rarely up to 3 cm. long. Sect. 5. MICROPHYLLUS.
- BB. Flowers in determinate racemes Sect. 4. STENOSTIGMA.

Subgenus I. *Gemmatus* (Koehne), stat. nov.*Philadelphus* subg. I. *Gemmatus* (Koehne), stat. nov.

Philadelphus Reihe 4. *Decorticatae pauciflorae* Koehne, Deutsche Dendr. 180, 184. 1893, pro parte.

Philadelphus sect. 1. *Poecilostigma* subsect. 1. *Gemmata* Koehne in Gartenfl. 45: 450. 1896, pro parte; et in Mitt. Deutsche Dendr. Ges. 1904(13): 77. 1904. — Engler, Pflanzenf. ed. 2, 18a: 191. 1930.

TYPE SPECIES: *P. mexicanus* Schlechtendal.

Flowers solitary, ternate, or in depauperate panicles; hypanthia obconic, or subglobose, generally dense pubescent; stamens about 40, rarely more or less; ovary semi-inferior, the stigma distinct, broadened or cris-

tate; capsules obovoid-ellipsoid or subglobose, the persistent calyx circumferential or subcircumferential; seeds long-caudate, the crowns with pointed lobes, erect or subscandent shrubs or vines; leaves evergreen or deciduous, remotely denticulate or serrate, triplinervate or quintuplinervate; petioles often twisted; axillary buds exposed.

This subgenus is strictly a Central American taxon. In the southern portion of its range there are several widely spreading species, and in the northern portion, the species are largely endemic to limited areas. It contains two sections including fourteen species. Their geographical distributions are as illustrated in Map 1.

Section 1. POECILOSTIGMA Koehne

Philadelphus subg. I. **Gemmatus** sect. 1. **Poecilostigma** Koehne in Gartenfl. 45: 450. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 77. 1904, pro parte.

Philadelphus sect. *Poecilostigma* Koehne, Il.cc. — Engler, Pflanzenf. ed. 2, 18a: 191. 1930.

Philadelphus Mexicani Rydb. in N. Am. Fl. 22: 164. 1905, in clavis, s. stat.

Philadelphus ser. *Gemmati* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 275. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949, pro parte.

TYPE SPECIES: *P. mexicanus* Schlechtendal.

Arching shrubs or vines, the current year's growth pubescent and usually verrucose, the axillary buds exposed; leaves remotely denticulate or serrate, the base rounded, 3- or 5-nerved, the apex acuminate, rarely acute; inflorescences depauperate panicles, or flowers solitary, the bracts linear or lanceolate, foliaceous; hypanthia subglobose or cyathiform, the sepals foliaceous, (5-) 8-20 mm. long; corolla usually disciform, often pubescent; stamens 40-50; disc conic, style (3-) 4-7 mm. long, the stigma broadened and cristate; fruit obovoid-ellipsoid; seeds long-caudate. Seven species, Mexico to Panama.

KEY TO THE SPECIES

- A. Flowers many on ramified branches; hypanthia subglobose.
 - B. Inflorescences loose, paniculate, the secondary axis of unequal length, 4-30 mm. long, the lower ones longer.
 - C. Hypanthia glabrous or with few weak pilose hairs; base of the hairs on the stem not thickened; axillary buds subglobose 1. *P. affinis*.
 - CC. Hypanthia pubescent; base of the hairs on the stem thickened; axillary buds conic.
 - D. Hypanthia lanate, the underneath tissue obscure; inside of the petals glabrous 2. *P. karwinskyanus*.
 - DD. Hypanthia villose, the underneath tissue visible; petals pubescent on the apical ends 3. *P. pueblanus*.
 - BB. Inflorescences compact, raceme-like, the secondary axis equal in length, 2-4 mm. long, the flowers crowded at the end of elongated leafy branches 4. *P. myrtooides*.

- AA. Flowers solitary or ternate; hypanthia cyathiform or obconic (except *P. glabripetalus*).
- B. Petals pubescent on both surfaces; hypanthia sparsely villose or pilose.
- C. Style and disc pubescent; axillary buds conic; leaves large, 5–11 cm. long, the petioles 8–10 mm. long 5. *P. mexicanus*.
- CC. Style and disc glabrous; axillary buds subglobose; leaves small, 1–3.5 cm. long, the petioles 2–3 mm. long 6. *P. austro-mexicanus*.
- BB. Petals glabrous, at least on the inside; hypanthia lanate 7. *P. glabripetalus*.



MAP 1. Geographical distribution of the species and sections of *Philadelphus* in the subgenus *Gemmatulus*.

1. *Philadelphus affinis* Schlecht. in *Linnaea* 13: 419. 1839. — Walp. *Rep.* 2: 151. 1843. — Hemsl. in *Biol. Centr. Am.* 1: 383. 1879. — Koehne in *Gartenfl.* 45: 487. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904(13): 78. 1904. — Schneider, *Ill. Handb. Laubh.* 1: 362. 1905. — Rydb. in *N. Am. Fl.* 22: 171. 1905. — Standl. in *Contr. U. S. Nat. Herb.* 23: 511. 1922. — Engler, *Pflanzenf.* ed. 2. 18a: 191. 1930.

Philadelphus zeyheri sensu Hemsl. in *Biol. Centr. Am.* 1: 384. 1880, non Schrader ex DC. 1828.

TYPE: Ehrenberg, Barranca de la Hacienda Del Carmen, S. Mexico.

An arching shrub or vine up to 4 meters high, the flowering branches slender, 10–20 cm. long, bearing 3 to 5 pairs of leaves, sparsely pilose, the base of the hairs not thickened; axillary buds subglobose, pubescent. Leaves ovate rarely ovate-elliptic, 4.5–8 cm. long, 2.5–4.5 cm. wide, rounded, rarely subcordate at the base, 5-nerved, acuminate at the apex, remotely serrate, each side with 2 to 5 teeth, subglobose or very sparsely strigose on both surfaces, more so on the principal nerves beneath, reticulations obscure above, conspicuous beneath, petioles 3–10 mm. long, pilose. Inflorescences depauperated panicles (Pl. V fig. 1) with 5-, rarely 3-, 1-, or 11-flowers, the woody part of the stalk 1–3 cm. long, pubescent as are the branchlets, bracts linear, the pedicels 2–3 mm. long, glabrous, after fruit up to 6 mm. long; hypanthia subglobose, 6 mm. in diameter, glabrous or with few weak pilose hairs, the sepals ovate, acuminate, 10 mm. long, 4–5 mm. wide, glabrous or very sparsely pilose; corolla subdisciform, 3.5–5 cm. across, the petals obovate to suborbicular, 1.3–1.8 cm. in diameter, glabrous, the apex round; stamens about 50, the longest three-fourths the length of the petals; disc subconic, glabrous; style 7 mm. long, undivided or the upper one-fifth separated, hirsute, the stigmas broadened, cristate, the abaxial surfaces broader and longer than the adaxial ones, the sterile portion hirsute (Pl. V fig. 1a). Capsules ellipsoid, the persistent calyx circumferential, the seeds long-tailed.

MEXICO: Hidalgo: Zacualtipán, *P. Maury* 5826 (NY), same locality, *H. E. Moore* 3238 (BH, G); in a barranca below Trinidad Iron Works, *C. G. Pringle* 8833 (F, G, MO, NY, US); Atotonilco, *Schiede*, June 1830 (A, US); Bluff above Cuera Humada, *A. J. Sharp* 4618 (TENN.). Tamaulipas: Tampico, Real del Monte, *M. Berlandier* 333 (F, MO, US). Without precise locality, Herb. Dendrol. *Schneider* (A).

The type not being available, this interpretation is made on the basis of Schlechtendal's original description and Koehne's supplementary remarks. Schlechtendal characterized the inflorescences as 5-flowered racemes, the peduncles and calyces smooth and glabrous. Unfortunately he did not mention the pubescence of the style. For this character I rely upon Koehne who certainly had access to the now destroyed type. According to Koehne the style of this species has loose stiff hairs. I therefore place the Mexican material with 5-flowered depauperate panicles, more or less glabrous hypanthia and calyces, and pubescent styles with *P. affinis* Schlecht. Hemsley in 1880 doubtfully published *Berlandier* 333 from Tampico as *P. zeyheri* Schrad. In this he mistook the material of a spontaneous Mexican species, *P. affinis* Schlecht., for a garden form cultivated in European gardens.

The ovate leaves, the subglobose glabrous hypanthia, the large foliaceous sepals with acuminate apices, the large number of stamens, the broadened stigmas and the ellipsoid capsules with circumferential persistent sepals of this species all suggest relationship to *P. inodorus* Linn. of the southern Appalachian region of the southeastern United States. As

the latter species has enclosed buds and this one has exposed buds their separation must have taken place far back in geological time.

In Mexico this species occurs on the Sierra Madre Oriental at altitudes of 1852–2000 meters, in regions where the annual rainfall attains at least 80 inches per year. Its white fragrant flowers appear from April to June. The specimens collected in July are with fruits.

2. *Philadelphus karwinskyanus* Koehne in *Gartenfl.* **45**: 486. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904(13): 1904. — Schneider, *Ill. Handb. Laubh.* **1**: 362. 1905. — Rydb. in *N. Am. Fl.* **22**: 170. 1905. — Standley in *Contr. U.S. Nat. Herb.* **23**: 311. 1922.

Philadelphus scandens Moore in *Bailey, Stand. Cycl. Hort.* **5**: 2582. 1916.

TYPE: Karwinsky, Tototapa, Oaxaca, Mexico.

A subscandent shrub up to 4 meters high, branchlets slender, the flowering ones over 50 cm. long, much ramified, terete, striate, villose, the base of the hairs thickened; axillary buds conic, villose. Leaves ovate, 4–7.5 cm. long, 2–3.5 cm. wide, rounded at the base, acuminate at the apex, 5-nerved, reticulations conspicuous beneath, remotely sharp serrate, 5–8 teeth on each side, sparsely strigose on both surfaces; petiole 5–10 mm. long, attached on cushion-like projections of the node. Inflorescences with 5–31 flowers, in a loose depauperate panicle, the woody portion below the pedicel 4–20 mm. long, pubescent, the pedicels 2–5 mm. long, thickly strigose and lanate; hypanthia subglobose, 4 mm. in diameter, strigose-lanate, the sepals ovate, 5–8 mm. long, densely lanate, the hairs entirely obscuring the tissue beneath; corolla 2.5–3 cm. across, the petals obovate-suborbicular 0.8–1.3 mm. in diameter, sparsely pubescent along the median dorsal line, glabrous on the ventral side, the apex rounded; stamens about 45, the longest half as long as the petals; disc subconic, pubescent, stigmas 2.5–3 mm. long, enlarged cristate, the sterile portion pubescent, the abaxial surface with 2 papillose ridges. Capsule and seed not known.

MEXICO: Oaxaca: Tepascalula, *Loesener* 1421(G); Huitzo, *L. C. Smith* 807(G). Vera Cruz: Orizaba, *F. Müller*, Jan. 1853(NY). Sinaloa: Mazatlan, *J. G. Ortega* 6770(F). Without precise locality, *Ortega* 7342(F).

UNITED STATES: Cultivated in California: Altadena, *F. W. Peirson* 79(BH); San Diego, *F. G. Woodcock* 870(F), 871(BH), 872(A, BH); Santa Monica, *L. H. & Ethel Bailey* 7804(BH); Los Angeles, *L. H. & Ethel Bailey* 9117(BH).

A great altitudinal variation is reported for this species. In Oaxaca it has been collected 2000 meters above the sea level and in Sinaloa, it has been reported from humid lowlands almost at sea level. It is an evergreen shrub, flowering all year around. In California where it is an introduced and cultivated species, flowering records cover August, October, December, January, February, March, April and May.

3. *Philadelphus pueblanus*, sp. nov.

Frutex subscandens, usque 4 m. altus, ramulis floriferis, 20–40 cm. longis, teretibus, striatis, 2–4 mm. diametro, dense pilosis et sparse strigosis, pilis basi incrassatis, gemmis axillaribus breviter, villosis; foliis ovatis, 4–7 cm. longis, 2–3.5 cm. latis, basi rotundatis, raro obtusis, quintuplinerviis, apice acuminatis, serratis vel subintegris, dentibus utrinque 1, 2 usque ad 5, utrinque strigosis, petiolo 5–10 mm. longo; inflorescentiis ramosis, 5- usque 31-floribus, pedunculis 4–20 mm. longis, pedicellis 3–6 mm. longis, villosis, verruculosus, hypanthiis subglobosis, 4 mm. diametro, villosis; sepalis ovatis, caudatis, 10 mm. longis, 4–5 mm. latis, sparse villosis; corolla disciformi, 4 cm. diametro, petalis oblongo-suborbiculatis, 2 cm. longis, 1.5 cm. latis, partibus medianis extus hirsutis, apice rotundatis et retusis; staminibus ca. 40; disco subconico, medio hirsuto; stylis 6–7 mm. longis, columnaribus indivisis; pubescentibus; stigmatibus cristatis, 2–3 mm. longis, partibus sterilibus hirsutis; capsulis et seminibus ignotis.

MEXICO: Puebla: vicinity of Puebla, *Bro. G. Arsène* (*Bro. Nicolas*) 171 (A, TYPE; G, MO, NY, US ISOTYPES); Arzobispado, *Bro. G. Arsène* 10136(US); Ixtaccihuatl, *C. A. Purpus* 169(MO, US); Com. Geogr.-Expl. Rep. Mexicana 1022(NY). Tlaxcala: Tlaxcala, *E. K. Balls* 4906(A). San Luis Potosí: Santa Barbara, *Bro. G. Arsène* 10093 (US). Mexico: Par Nicolas, *M. Bourgeau* 995(US); Temascaltepec, Rincón, *G. B. Hinton* 2362(A), 5032(BH, NY, US). Michoacan: Zitacuaro, *G. B. Hinton* 13342(G, NY, US). Morelos: near Cuernavaca, *J. N. Rose & W. Hough* 4412(US).

This species is intermediate between *P. affinis* Schlecht. which has glabrous or subglabrous hypanthium and *P. karwinskyanus* Koehne in which the hypanthium is thickly lanate with the indumentum entirely covering the epidermal tissue. In Puebla it occurs at altitudes between 1700 and 2194 meters as semiscandent shrubs in thickets and among trees in ravines. Its pale yellow sweet-scented flowers appear from March to October.

4. *Philadelphus myrtoides* Bertol. Fl. Guatim. 21. pl. 7. 1840. — Walp. Rep. 2: 151. 1843. — Hemsl. Biol. Centr. Am. 1: 383. 1879. — Koehne in Gartenfl. 45: 487. 1896. — Rydb. in N. Am. Fl. 22: 170. 1905. — Engler, Pflanzenf. ed. 2, 18a: 192. 1930. — Standley in Field Mus. Nat. Hist. Bot. Ser. 18: 474 (Fl. Costa Rica), 1937.

Philadelphus trichopetalus Körnicke in Gartenfl. 16: 73. 1867. — Koehne in Gartenfl. 45: 487. 1869; et in Mitt. Deutsch. Dendr. Ges. 1904(13): 78. 1904. — Smith in Pittier, Prim. Fl. Cost. II. 1: 90. 1898. — Schneider, Ill. Handb. Laubh. 1: 364. 1905. — Engler, Pflanzenfam. ed. 2, 18a: 192. 1930.

Philadelphus mexicanus sensu Moore in Bailey, Stand. Cycl. Hort. 5: 2582. 1916, pro parte. — Standley & Calderón, Pl. Salv. 88. 1925, non Schlechtendal.

Philadelphus sempervirens Hort. ex. Moore in Bailey. Stand. Cycl. Hort. 5: 2582. 1916.

Philadelphus matudai Lundell in Contr. Univ. Mich. Herb. 4: 6. 1940.

TYPE: Botanical Garden of Bologna, Italy.

An arching shrub, 2–4 m. high, flowering branches slender, 21–50 cm. long, with 14 or more pairs of leaves, longitudinally striate, rather densely villose, the trichomes slightly curled, their base more or less thickened; buds small, rounded, densely brown villose. Leaves ovate, 3–4 cm., rarely up to 5.5 cm. long, 1–2.8 cm. wide, sparsely strigose above, more so beneath, the hairs glandular at the base, rounded or rarely obtuse at the base, acuminate at the apex, subentire, or remotely denticulate, with 2 to 6 sharp teeth projecting outward on each side, triplinervate or quintuplinervate, reticulations obscure on both surfaces; petioles 6–9 mm. long, strigose. Flowers 5, rarely 1, 3, or 7, crowned at the end of long slender branchlets, the woody portions below the pedicels uniformly short, 2–4 mm. long, the bracts linear, 5–13 mm. long, the pedicels 3–4 mm. long, white lanate; hypanthia subglobose, 5 mm. in diameter, densely lanate; sepals ovate, acuminate, 8 mm. long, 4 mm. wide, lanate; corolla disciform, 3–4 cm. in diameter, the petals suborbicular-ovate, 1.2–1.8 cm. long, 1.1–1.7 cm. wide, slightly hirsute along the median longitudinal line on both surfaces, the apex rounded; stamens ca. 44, the longest half as long as the petals; disc subconic, pubescent, the style 3–4 mm. long, pubescent, the stigmas 3 mm. long, enlarged, cristate, the abaxial surface as long as the adaxial, the sterile portions hirsute; capsules and seeds not known.

MEXICO: Chiapas: Volcano Tacana, *E. Matuda* 2791 (ISOTYPE of *P. matudai* Lundell, A, F, G, NY, US).

GUATEMALA: Alta Vera Paz: Vicinity of Cobán, *P. C. Standley* 92452(F). Guatemala: near Finca La Aurora, *Ignacio Aguilar* 82(F). Huehuetenango: near Chiantla, *P. C. Standley* 82517(F). Sacatepéquez: near Antigua, *P. C. Standley* 60316(F); *S. Hayes* (G). Quezaltenango: *P. C. Standley* 86561(F, US). Suchitepéquez: vicinity of Finca Alvidas, *J. A. Steyermark* 35458(F).

EL SALVADOR: San Salvador: *S. Calderón* 687 (F, G, US, MO, NY); *M. C. Carlson* 435(F). Ahuachapán: near Ataco, *P. C. Standley* & *V. E. Padilla* 2726(F).

HONDURAS: Morazan: Tegucigalpa, *J. V. Rodríguez* 3173(F).

COSTA RICA: Cartago, Cervantes, *A. Tonduz* 10444(US); San José. *Tonduz* 1492(US); Las Cónavas, *P. C. Standley* 36006(US); Tapisca de Zaruro, *Austin Smith* 185(US).

PANAMA: Chiriqui: vicinity of Bajo Mona and Quebrada Chiquero, *R. E. Woodson* & *R. W. Schery* 588(MO).

CULTIVATED: California: Santa Barbara, *E. P. Bradbury*, Oct. 10, 1915(BH).

The identification of this species is based on Bertoloni's description and illustration. In his illustration he characterized *P. myrtoides* as a plant

with rather small ovate-elliptic leaves on the flowering branches which terminate with crowded cluster of several flowers each in the axil of a reduced leaf. Among the available collections of Guatemalan *Philadelphus*, Bertoloni's description and illustration conforms in all respects to Standley 60316, 82417 and Steyermark 35458. It is also well represented by Calderón 687 from El Salvador. Matuda 2791 represents the northern limit of the range of the species. Bradbury's collection from Santa Barbara, in Bailey Hortorium, was identified as *P. sempervirens* Hort. This specimen was probably Moore's material basis for the publication of his *P. sempervirens*.

Although 110 years have elapsed since *P. myrtoides* was published, it has not been well understood. Körnicke was probably not aware of Bertoloni's species when he published *P. trichopetalus* from Costa Rica. According to his description the Costa Rica plant has flowers clustered at the end of a branchlet, and the petals of the flowers are softly pilose. I have not seen Körnicke's type. But judging from the Costa Rica and Panama collections I have examined and by our present knowledge of the distribution of the various species of *Philadelphus* in Central America, *P. trichopetalus* Körnicke and *P. myrtoides* Bertol. are conspecific.

Philadelphus myrtoides is the most southern species of the genus. It has been collected on the high mountains from Chiapas in Mexico through Guatemala, El Salvador, Honduras south to Costa Rica and Panama. In Guatemala it occurs in cypress groves at altitudes ranging from 1200 to 1930 meters. Standley suggested the possibility of it being introduced and cultivated in Costa Rica. Some of the El Salvador collections were from gardens. Apparently this species has been widely cultivated in Central America where it flowers from January to August. The creamy white fragrant flowers are sold in the markets for decorative purposes under the name "Mosqueta."

Philadelphus myrtoides is closely related to *P. karwinskyanus* Koehne but the latter species can be distinguished for its elongated peduncles and its petals being glabrous on the inner surface.

5. *Philadelphus mexicanus* Schlecht. in Linnaea 13: 418. 1839. — Walp. Rep. 2: 151. 1843. — Hemsley in Biol. Centr. Am. 1: 384. 1879, excl. spec. Seemann, Coulter, Ghiesbreght. — W. G. Smith in Gard. Chron. n.s. 19: 753, fig. 123. 1883. — Burbidge in Gard. Chron. III. 34: 218, fig. 89. 1903. — Hook. f. in Bot. Mag. 124: pl. 7600. 1898. — Koehne in Gartenfl. 45: 487. 1896; et in Mitt. Deutsch. Ges. 1904(13): 78. 1904. — Wittmack in Berl. Gartenz. 1883: 528, fig. 91. 1883. — Dippel, Handb. Laubh. 3: 335. 1893. — Schneider, Ill. Handb. Laubh. 1: 362, fig. 234 b-b.² 1905. — Rydb. in N. Am. Fl. 22: 170. 1905. — Standley in Contr. U. S. Nat. Herb. 23: 311. 1922. — Rehder, Man. Cult. Trees Shrubs 280. 1927, ed. 2, 275. 1940; et Bibliogr. Cult. Trees Shrubs 195. 1929. — Hansell, Mexico Pl. 162. 1935. — Bean, Trees Shrubs ed. 7, 2: 419. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

A scandent evergreen shrub to 5 meters high with long drooping branches, the second year's growth 3–4 mm. in diameter, castaneous, rugose, the bark closed, longitudinally rimulose, the current year's growth 1.5–2 mm. in diameter, hirsute, the trichomes with more or less thickened bases; axillary buds conic, the first few below the flowers often developing into virgin shoots. Leaves ovate, 5–11.5 cm. long, 2–5 cm. wide, very sparsely strigose on both surfaces, rounded or obtuse or subcordate at the base, 5- or rarely 3-nerved, acuminate at the apex, subentire or with 1 to 6 tooth-like projections on each side, reticulations obscure above, conspicuous beneath, the petioles 8–10 mm. long, strigose. Flowers solitary, yellowish white, very fragrant; pedicels hirsute, 1–3 mm. long, bracts lanceolate, 1–2 cm. long; hypanthia cyathiform, sparsely villose, the trichomes slightly curly; sepals foliaceous, ovate, long acuminate or cordate, 10–20 mm. long, 7 mm. wide, sparsely villose, the hairs tending to curl slightly; corolla 3–4 cm. across, the petals suborbicular, hirtellous on both surfaces; stamens ca. 40, the anthers oblong; disc subconic, hirsute at the center, the styles 3 mm. long, pubescent, the upper half divided, the stigmas 3 mm. long, cristate, the abaxial surface much longer than the adaxial one, the sterile portion often hairy. Capsules obovoid-ellipsoid, the lower portion near the base quadrangular, about 12 mm. long, 10 mm. in diameter, the persistent calyx subcircumferential. Seeds long-caudate.

MEXICO: Mexico: Amecameca, *G. L. Fisher* on July 29, 1924(F, MO, US); Federal District, *A. J. Sharp* 445 (A, TENN); Mts. of Toluca, Halstead (NY). Guerrero: Omiltemé, *A. J. Sharp* 441551 (A, TENN). Michoacán: Morelia, Cerro Azul, *Bro. G. Arsène* 5141 (F, G, MO, US). Oaxaca: Cerro de San Felipe, *C. Conzatti & V. Gonzalez* 471(G); *H. Galeotti* 2850(US); *E. W. Nelson* 1398(G, US). Chiapas: Siltepec, *E. Matuda* 1701(A, MO, US). Vera Cruz: Jalapa, *S. Schiede* (G, NY, ISOTYPES); Orizaba, *Botteri* 1105(G, US). Puebla: Cero Guadalupe, *Nicolas*, June 10, 1909(F).

GUATEMALA: Huehuetenango: San Juan Ixcoy, *A. J. Sharp* 4616(F); definite locality not given, *J. D. Smith*, April 9, 1896(G); Cerro Cananá, Sierra de los Cuchuatanes, *J. A. Steyermark* 49059(F); Aguacatán, *P. C. Standley* 91218(F). Quezaltenango: Volcán de Santa Maria, *P. C. Standley* 83535(F); *J. A. Steyermark* 33985(F); Palestina, *P. C. Standley* 84230(F); Santa Maria de Jesús, *P. C. Standley* 84860(F); above Mujuliá, *P. C. Standley* 85608(F, US); Zunil, *P. C. Standley* 85647(F); Volcán Santo Tomas, *J. A. Steyermark* 34952(F). Quiché: *O. F. Cook* 31(US); San Miguel Uspantán, *Heyde & Lux* (distributed by *J. D. Smith*) 3046(G, NY, US); Chajul, *A. J. Sharp* 4681(F). Sacatepequez: Volcán de Auga, *P. C. Standley* 65124(F). Chimaltenango: Santa Elena, *D. S. Johnson*, Aug. 10, 1932(F); *A. F. Skutch* 335 (A, US). Sololá: Volcán San Pedro, *J. A. Steyermark* 47253(F, US); Volcán Atitlán, *J. A. Steyermark* 47527(F). San Marcos: Volcán Tajumulco, *J. A. Steyermark* 35661(F). Without precise locality, *F. C. Lehmann*, June 1882(US).

CULTIVATED: California: Berkeley, in the garden of A. Blake, *N. F. Bracelin*, 1354(BH).

As the natives of Mexico had cultivated species of *Philadelphus* from early times it is inevitable that certain garden forms had been produced by them. It happened that the first published Mexican species was based on a double flowered form. Schlechtendal cited three specimens, Schiede from Jalapa, Mühlenpfordt from Oaxaca and a specimen from Mexico in Herb. Lehmann. Of these I have seen only the duplicates of Schiede's collection, which agree with Schlechtendal's description. Thus the double flowered form typifies the species. Apparently this form is found only or chiefly in the states of Vera Cruz and Puebla where the mean annual temperature is between 62–67° F. and the mean annual rainfall is 40–80 inches. The Bracelin collection is the only specimen from a cultivated plant outside of Mexico that I have seen. It has been reported that the cultivated plants climb to 12 meters and their flowers are yellowish or deep cream white.

Specimens collected from the wild population all have simple flowers. Compared with the isotypes of typical *P. mexicanus* Schlecht., I can detect no other characters from the above cited specimens to distinguish them as a form besides their possession of the simple flowers. Like the double-flowered form, their petals are pubescent on both surfaces, the disc and style are pubescent, and the hypanthium is sparsely villose with the trichomes slightly curled. In general, their leaves are larger and more prominently quintuplinervate than the double flowered form. But this 5-nerved condition is also true with the large leaves of the cultivated specimens. It seems that with both the wild and the cultivated material, at the base of each leaf, there is a pair of small nerves originated from the petiole and running along the basal portion of the margin. When the leaves are small, these nerves are so closely pressed against the margin that they appear inconspicuous.

In Mexico this species occurs at altitudes of 2280–3000 meters in Oaxaca. In Huehuetenango, it has been recorded at altitudes of 1950–3160 meters on steep limestone slopes of damp oak forests. In Quezaltenango it occurs at altitudes of 1500–3000 meters in sunny thickets, damp sandy hillside forests or in wet brushy ravines as subscandent shrubs. In Sololá it occurs in damp cloud forests.

The vernacular names reported are "Mosqueta" and "Azahar," the former more widely applied. Hernandez (1651) in "Nova Plantarum Mexicanorum Historia" discussed and illustrated a plant with opposite leaves and a cluster of two simple flowers under the name, *Acuilotl* or *Volubili Aquatica*. He mentioned it as growing in wet places, creeping on the ground or scrambling up trees. This record has been regarded by Schlechtendal, Lindley, Hooker and many modern authors as representing *P. mexicanus* Schlecht. To the Mexican Indians this species is economically rather important. They employ the flowers both in preparing perfume and for making garlands. The leaves are taken in wine for the relief of colic, or crushed and applied as a plaster to ease strained members and dissolve tumors.

The pubescent petals and simple flowers of this species resemble those

of the flowers of *P. myrtoides* Bertol. But the latter species can be readily distinguished by its clustered flowers and densely lanate hypanthium.

6. ***Philadelphus austro-mexicanus*, sp. nov.**

Philadelphus mexicanus sensu Decaisne in Rev. Hort. III. 1: 381, fig. 20. 1852. non Schlechtendal. 1839.

Frutex ramosissimus, ramulis floriferis brevibus, ca. 3 cm. longis. 1 mm. diametro, castaneis, rugoso-strigosis, pilis basi incrassatis, gemmis axillaribus subglobosis, pilosis; foliis ovatis vel ovato-lanceolatis, 1–3.5 cm. longis, 0.5–1.5 cm. latis, basi subrotundatis, triplinerviis, apice subacuminatis vel acutis, serratis, utrinque 1- usque 5-serratis utrinque sparse strigosis vel praeter nerviis subglabris, petiolo 2–3 mm. longo; floribus solitariis, pedicellis 2 mm. longis, strigosis; hypanthiis obconicis, 3 mm. longis, 4 mm. diametro, sparse pilosis; sepalis ovatis, 9–11 mm. longis, caudatis, sparse pilosis vel subglabris; corolla disciformi, 3.8–4 cm. diametro, petalis obovatis, 1.5–1.7 mm. longis, 1.3 mm. latis, utrinque in partibus medius hirsutis; staminibus ca. 52, disco glabro, stylis 4 mm. longis, glabris, partibus superioribus liberis, stigmatibus dilatatis, cristatis; capsulis et seminibus ignotis.

MEXICO: Chiapas: *Dr. Ghiesbreght 813* (G. TYPE; F, MO, ISOTYPES; A, fragment of ISOTYPE).

The rugose branchlets, the dentation of the leaves, the large sepals, the pubescent petals, the numerous stamens, the divided style and the dilate-cristate stigmas of this species all suggest a close relationship to *P. mexicanus* Schlecht. But it can be readily distinguished by its small leaves, very sparsely pilose hypanthium and sepals and its glabrous styles.

Decaisne's figure represents a plant with small leaves. His concept of Schlechtendal's species was apparently based on a Ghiesbreght collection, very likely a part of the same collection of which three specimens are available to me. All of them have small leaves and glabrous styles.

7. ***Philadelphus glabripetalus*, sp. nov.**

Philadelphus mexicanus sensu Lindl. Bot. Reg. 26(Misc.): 37. 1840; et 28: pl. 38. 1842. — sensu Hemsl. in Biol. Centr. Am. 1: 384. 1879, pro parte, non Schlechtendal, 1839.

Frutex ramosissimus, ramulis floriferis 5–15 cm. longis, 1–1.5 mm. diametro, rugoso-hirsutis, pilis basi incrassatis; foliis ovatis vel ovato-lanceolatis, 1.5–6 cm. longis, 1–2.5 cm. latis, basi rotundatis, triplinerviis, apice acuminatis, subintegris vel serratis, dentibus utrinque 1 vel 2, raro 4, supra subglabris vel sparse villosis, subtus sparse villosis; petiolo 3–5 mm. longo, villosio; floribus solitariis vel raro ternatis, pedicellis 3–5 mm. longis, dense villosis, hypanthiis subglobosis, 5 mm. diametro, lanatis; sepalis ovatis, 10–15 mm. longis, 5 mm. latis, acuminatis; corolla 2.5–3 cm. diametro, petalis obovatis, vel suborbicularibus, 1–1.3 cm. longis, 9–10 mm. latis, utrinque glabris, vel extus hirsutis, staminibus ca. 60;

disco medio hirsuto, stylis glabris vel basi hirsutis, 3–4 mm. longis, stigmatibus cristatis, 4 mm. longis, supra liberis; capsulis et seminibus ignotis.

MEXICO: Federal District: Sierra de Ajusco, C. G. Pringle 6311(A, TYPE: G. MO. NY. U.S. ISOTYPES). Puebla: Moria, Nicolas, in February 1908(F). Without precise locality, *P. Maury* 3158(NY), 3822(NY).

The shape of the leaves, the solitary flowers and the glabrous petals suggest a relationship to *P. osmanthus* S. Y. Hu, but the latter species has strigose lower leaf-surfaces and hypanthia, and short styles while the present species has villose lower leaf-surfaces, lanate hypanthium, and styles 3–4 mm. long. It differs from *P. mexicanus* Schlecht. in having glabrous petals and smaller leaves. Its solitary or ternate flowers also suggest relationship with *P. coulteri* S. Wats. but the latter species has densely villose hypanthia with the epidermis entirely obscured. In the Federal District, this species occurs at altitudes 2400–2470 meters. It climbs among shrubs up to 5–7 meters high. Specimens collected from June to September all bear flowers. This suggests that like many other Mexican *Philadelphus*, this species has a very long flowering period; of course, local climatic conditions may be involved.

Judging by the figures and the descriptions given by Lindley (1842), his material which was introduced by Hartweg from the Hacienda del Carmen, could not be the true *P. mexicanus* Schlecht. for it has small leaves and a glabrous style while Schlechtendal's species has large leaves and a pubescent style. As Lindley described the hypanthium and calyx of his material as densely pubescent, this eliminates the possibility of it being *P. austro-mexicanus* S. Y. Hu which is another small-leaved Mexican species, for the latter has more or less glabrous hypanthium and calyx, and pubescent style. By the process of elimination, one may logically come to the conclusion that the material Hartweg introduced to the European gardens belongs here.

Section 2. *Coulterianus*, sect. nov.

Philadelphus subg. I. *Gemmatus* sect. *Coulterianus*, sect. nov.

TYPE SPECIES: *P. coulteri* Wats.

Frutex erectus vel subscandens, ramulosis hornotinis pubescentibus, plerumque verrucosis, gemmis axillaribus expositis; foliis integris, raro denticulatis vel inconspicue serratis, basi rotundatis vel obtusis, raro acutis, triplinerviis; apice acutis vel obtusis; floribus solitariis vel raro ternatis; hypanthiis subglobosis, pubescentibus; sepalis ovatis, 3–8 mm. longis, corolla cruciformi vel disciformi; staminibus 30 usque ad 44; disco plano, stylo 1–3 mm. raro 4 mm. longo, stigmatibus noncristatis; capsulis subglobosis; seminibus longo-caudatis.

Seven species, all in northeastern Mexico.

KEY TO THE SPECIES

A. Lower leaf-surface pilose or strigose; stems rugosely hirsute, the base of the trichomes thickened.

- B. Hypanthia pilose, the epidermal tissue visible; the lower leaf-surface pilose8. *P. osmanthus*.
- BB. Hypanthia densely villose, the epidermal tissue obscure; the lower leaf-surface strigose.
- C. Leaves oblong; pedicels 5–8 mm. long; petals emarginate at the apex9. *P. oblongifolius*.
- CC. Leaves ovate; pedicels 2–3 mm. long; petals rounded at the apex.
- D. Style and center of disc pubescent; leaves on flowering shoots 2–3 cm. long10. *P. coulteri*.
- DD. Style and center of disc glabrous; leaves on flowering shoots 1–2 cm. long.11. *P. asperifolius*.
- AA. Lower leaf-surface densely villose; stem pilose, the base of the trichomes not thickened.
- B. Leaves subcoriaceous, hispid above, densely villose and appearing white beneath.
- C. Style pubescent12. *P. sargentianus*.
- CC. Style glabrous13. *P. pringlei*.
- BB. Leaves characeous, weakly pilose above, very sparsely villose beneath; style glabrous14. *P. callicolus*.

8. *Philadelphus osmanthus*, sp. nov.

Frutex subscandens, 1.3 m. altus, ramosissimus; ramis robustis, 3–5 mm. diametro, fumeis, longitudinaliter rimulosis, bienniis 2 mm. crassis, castaneis, striatis, rugoso-hirsutis, corticibus clausis, hornotinis 1–1.5 mm. diametro, pilis basi incrassatis, gemmis conicis, strigosis, pilis luteis; foliis ovatis, raro ovato-lanceolatis, 2–6 cm. longis, 0.8 cm. latis, basi obtusis, apice acutis vel obtusis, apiculatis, integris vel utrinque 1 vel 3 serrulatis, utrinque strigosis, pilis eburneis, petiolo 4–9 mm. longo; floribus 1, raro 3, terminalibus, bracteis linearibus, 3–10 mm. longis, pedicellis 5–10 mm. longis, cum hypanthiis et calycibus incano-pilosis, hypanthiis subglobosis, 5–7 mm. diametro; sepalis ovatis, acuminatis, 7–8 mm. longis; corolla subcruciformi, 2.5–3.2 cm. diametro, petalis obovatis, apice emarginatis, 1.2–1.5 cm. longis, 0.7–1.2 cm. latis; staminibus ca. 36; disco medio piloso, stylo brevissimo, 1 mm. longo, vix hirtello, stigmatibus 3 mm. longis, cristatis, supra divisis; capsulis ellipsoideis vel subglobosis, 6–8 mm. diametro, calycibus persistentibus supra medium affixis; seminibus longocaudatis.

MEXICO: Hidalgo: Jacala, V. H. Chase 7310 (NY, TYPE; A, F, G, MO, ISOTYPES).

This species occurs in woods in deep ravines at an altitude of 1525 meters. Unlike other species of the genus, the lateral buds on the branchlets of this one are suppressed from normal development. Thus its flowering shoots are largely developed from the terminal buds, a very unusual character in *Philadelphus*. The thickened base of the epidermal hairs on the branchlets, the elongate stigmas and the pubescent disc of this species suggest relationship to *P. coulteri* Wats. The latter species can be dis-

tinguished by the thickly villose hypanthium. The subentire leaves sparsely strigose and the long-tailed seeds of this species also suggest a remote relationship with the southern Appalachian species *P. inodorus* Linn. which has enclosed axillary buds. The very short style conforms to Körnicke's description of *P. asperifolius*, a species with glabrous style and disc.

9. *Philadelphus oblongifolius*, sp. nov.

Frutex ramosissimus, ramis cinereis, ramulis gracilibus, bienniis 1–1.5 mm. crassis, brunneis, verrucoso-hirsutis, hornotinis 1 mm. diametro, pilis basi incrassatis; foliis oblongis, raro oblongo-ovatis, 1.3–2.5 cm. longis, 4–8 mm. latis, utrinque obtusis, apice apiculatis, margine integerrimis, utrinque strigosis, pilis subtus longioribus et densioribus, petiolo 3 mm. longo; floribus solitariis, pedicellis 6–8 mm. longis, incanis, hypanthiis calycibusque incanis; sepalis ovatis, 6 mm. longis, 2.5–3 mm. latis; corolla cruciformi, 3.5 cm. diametro, petalis obovatis, apice emarginatis, 1.6 cm. longis, 1.1–1.4 cm. latis; staminibus ca. 30; disco praeter medio glabro, stylo 5 mm. longo, supra diviso, basi dense hirsuto, stigmatibus 2 mm. longis. Capsulis ignotis.

MEXICO: San Luis Potosi: Minas de San Rafael, C. A. Purpus 5368b (A, fragment of TYPE; F, TYPE; MO, NY, ISOTYPES).

Through its strigose trichomes on the leaves, and pubescent styles this species is closely related to *P. Coulteri* Wats. It can be distinguished from *P. coulteri* by its slender branchlets, oblong leaves, long pedicellate flowers with emarginate petals and 5 mm. long styles.

10. *Philadelphus coulteri* Wats. in Proc. Am. Acad. 22: 472. 1887.

Philadelphus purpusii Brandegee in Univ. Calif. Publ. Bot. 4: 270. 1912.

TYPE: Dr. Coulter 77, Zimapan, Mexico (Gray Herbarium).

A subscandent shrub, the branches ferrugineous, the second year's growth 2–3 mm. in diameter, the bark rugose, closed, slightly longitudinally rimulose; the current year's growth rugose and hirsute, the trichomes with thickened bases. Leaves ovate, or ovate-elliptic, subentire, obtuse or acute, apiculate, rounded or rarely obtuse at the base, strigose on both surfaces, more so beneath, those on the flowering branches, 1.5–3 cm. long, 1–1.5 cm. wide, the petioles 3–4 mm. long. Flowers solitary, rarely ternate, the pedicels 2–3 mm. long, thickly villose and white like the hypanthia and calyx, the sepals ovate, 5–6 mm. long; corolla disciform, 2.5–3 cm. across, the petals orbicular-obovate, rounded at the apex; stamens 34–38; disc pubescent at the center, the style 2–3 mm. long, the upper half divided, the stigmas 2–2.5 mm. long, the abaxial surface papillose, 2 mm. long, the adaxial surface half as long. Capsules and seed not known.

MEXICO: Hidalgo: Zimapan, *Dr. Coulter* 77 (G, TYPE); woods above Minas Viejas between Zimapan and Jacala, *H. E. Moore, Jr.* 2767 (G, BH); Atotonilco, *Schiede*, June 1830 (NY). San Luis Potosi: Minas de San Rafael, *C. A. Purpus* 4910 (MO), 5368 (F, G, MO, US ISOTYPES of *P. purpusii* Brandegees; A, photo and fragment). Tamaulipas: near Frank Harrison's "Rancho del Ciel" in Sierra de Guatemala above Gomez Tarias, *Sharp, Shank, Wolfe & Hernandez* 52201 (A, TENN), 52060 (A, TENN).

Philadelphus coulteri Wats. was essentially based on *Coulter* 77 collected from Zimapan. In publishing the species Watson also cited C. S. Sargent's collection from Monterey. As the species was named after Coulter, his number 77 in the Gray Herbarium should be the actual type of the species. Sargent's material is specifically distinct. It differs from the type of *P. coulteri* in having smooth pilose branchlets, leaves hispid above and densely long villose beneath and a very short style. In 1888 Watson published an illustrated account of *P. coulteri*. As Coulter's collection is rather fragmentary, that illustration was unfortunately drawn from Sargent's material. This publication has an out-reaching misleading effect in the identification of the true *P. coulteri* among botanists as well as horticulturists and consequently cytogeneticists.

Philadelphus coulteri Wats. was first collected in Zimapan. Additional material extends its range northward to Gomez in the State of Tamaulipas. At this area, the southeastern end of the Mexican Central Plateau, the plant grows, according to Moore, as a shrub a little over a meter high and its flowers are white, and fragrant. The standard reference books on cultivated shrubs have recorded this species as having purple-centered flowers. This is apparently incorrect.

Watson published this species in 1887 on the basis of a herbarium specimen. He did not know the flower color, nor did he indicate it in the description. The next year an illustrated account was published in *Garden and Forest*. Here no flower color was mentioned either. Three years later, Burbidge wrote Hemsley from Dublin, Ireland, saying, "Can you kindly give me the name of the enclosed? I cannot find it in the books. It exists in one or two old gardens here, where it is called Rose Syringa. Its sweet fragrance and purple-centered flowers are remarkable." What Hemsley reported we do not know, but this was later referred to *P. coulteri*. Meanwhile, Nicholson in the *Supplement to the Garden Dictionary* incorporated Watson's review of *P. coulteri* from the *Garden and Forest*. At the end of his summary Nicholson put down 1888, the year when his source material was published, as the year of the introduction of the plant into cultivation. Burbidge got this reference and in 1903 he published a note saying "There is a variety of *P. mexicanus* called *P. M. Coulteri*, introduced, it is said in Nicholson's *Supplement*, as recently as 1888; but probably this is a mistake as the shrub has existed for many years in old Irish gardens, where it is known as the "Rose Syringa" . . . and it differs from all other species or varieties . . . each of its four white petals has a purplish blotch at its base." This is a misinterpretation of Watson's figure and description and also a misidentifica-

tion of the Irish "Rose Syringa." But since that time in all major works on cultivated shrubs and even in books dealing principally with the flora of Mexico, the error in the flower color of *P. coulteri* Wats. has been perpetuated.

Claims have been made by hybridizers and cytogeneticists that *P. coulteri* Wats. is a grandparent of the triploid garden hybrids, "Belle Etoile," "Sybille" and "bicolor" which are segregates of *P. purpureo-maculatis* Lemoine.¹ There seems to be no record that true *P. coulteri* has ever been introduced into cultivation, thus it is impossible for it to have been a parent of *P. purpureo-maculatus* Lemoine. The above mentioned claims do not seem to have any material support. The Monterey region is better known botanically than Zimapan, the type locality of *P. coulteri*. Consequently the *Philadelphus* that Sargent collected is much better represented in American herbaria than is true *P. coulteri*. It was almost inevitable that these specimens should have been mistaken for *P. coulteri*. When typical *P. coulteri* Wats. was again collected by Purpus in 1911. Brandegee was misled into creating a new binomial, for *P. purpusii* Brandegee is the genuine *P. coulteri* Wats. *Purpus* 5368, the type number of *P. purpusii* Brandegee represents an aggregate of three elements, probably three separate collections combined under one number of which I have examined five sheets. The element with glabrous disc and style belongs to *P. asperifolius* Körnicke. The two other elements both have a pubescent disc and style. One of them has ovate leaves and styles shorter than the stigmas. This one agrees with Brandegee's description of *P. purpusii*, and is identical with the type of *P. coulteri* Wats. The other element has small oblong leaves and elongated style which is longer than the stigmas. It becomes the type of *P. oblongifolia* S. Y. Hu.

11. *Philadelphus asperifolius* Körnicke in Gartenfl. 16: 73. 1867. — Koehne in Gartenfl. 45: 487. 1896; et in Mitt. Deutsche. Dendr. Ges. 1904(13): 78. 1904. — Schneider, Ill. Handb. Laubh. 1: 364. 1905. — Rydb. in N. Am. Fl. 22: 171. 1905. — Standl. in Contr. U.S. Nat. Herb. 23: 310. 1922.

TYPE: *Karwinsky* July 1842, Hacienda Santyaguillo, Mexico (Herb. Hort. Petropol.).

An elegant shrub, 2–3 meters high, branchlets rigidly hirsute, the second year's growth gray, longitudinally rimulose, the bark closed, the current year's growth brown, pubescent, the hairs with thickened bases. Leaves ovate, those on the vegetative shoots up to 3 cm. long, 1.3 cm. wide, those on the flowering shoots 1.3–1.7 cm. long, 0.5 cm. wide, rounded at the base, obtuse and apiculate or subacute at the apex, both surfaces sparsely covered with rigid, straight appressed white hairs, the petioles 1–2 mm. long. Flowers solitary, subsessile, the pedicels 1–3 mm. long, canescent as are the hypanthia and the calyx, the sepals ovate, 3 mm. long; corolla disciform, 1.5–2 cm. across, the petals obovate, rounded at

¹ E. K. JANAKI AMMAL in Jour. Roy. Hort. Soc. 76: 272. 1951.

the apex, twice the length of the sepals; stamens 30–38; disc glabrous, the style short, about 1.5 mm. long, undivided, glabrous, the stigmas separated, 2 mm. long, the abaxial surface twice as broad and as long as the adaxial one. Capsules subglobose, 6–7 mm. long, 7 mm. diameter, the persistent calyx subapical. Seeds long-tailed.

MEXICO: San Luis Potosi: Minas de San Rafael, C. A. Purpus 4910 (A, F, G, US), 5368a (G, MO, NY, US).

Unable to examine the type, the identification of this species is based on the original detailed description published by Körnicke and the diagnostic characters supplemented by Koehne who probably saw the type or an isotype. Körnicke described the species as having ovate or broad-elliptic leaves which are obtuse and apiculate or subacute at the apex, and about 3 cm. long and 1.5 cm. wide on sterile shoots. He did not mention the nature and position of the buds and the presence or absence of hairs on the style. For these characters we have to rely upon Koehne's observations. In his latest synopsis of the genus, under the subsection Gemmati which was characterized as having a smooth almost obsolete and glabrous style he placed *P. asperifolius* and *P. serpyllifolius* Gray. Judging from the style of the latter species, the type of which is before me, Koehne's characters indicate a species in which the styles are short but definitely present, 0.5–1.5 mm. long. By inference, Körnicke's description, which calls for no style and the stigmatic column thick and subsessile, may also be interpreted to apply to flowers with short but definite styles. One of the elements of *Purpus* 5368, which I have indicated as 5368a, has small ovate leaves, 0.5–1.7 cm. long, 0.4–0.7 cm. wide on the flowering shoots, and glabrous styles. These characters conform to Körnicke's description of the leaves and Koehne's diagnosis of the style of *P. asperifolius*, thus I interpret that element as representing Körnicke's species. *Purpus* 4910 is a poorly selected fruiting specimen. With the exception of one, all sheets I have examined are sterile, and the only fertile specimen has just one fruit with a broken top. The branching is much looser than is that of *Purpus* 5368a. The leaves seem to fit Körnicke's description of those on the vegetative shoots. The small part of the disc left on the broken fruit appears to be glabrous.

The ovate shape of the strigose leaves, the densely villose hypanthia and the very short pedicel of the flower of this species suggest a very close relationship with *P. coulteri* Wats. Yet it can be readily distinguished from Watson's species by its glabrous disc and style and its rather small leaves on the flowering shoots which are only 1–2 cm. long. *Philadelphus coulteri* Wats. has a pubescent disc and style, with the leaves on the flowering shoot 2–3 cm. long. The fragrant white flowers of this species appear in June.

12. *Philadelphus sargentianus*, sp. nov.

Philadelphus coulteri Wats. in Proc. Am. Acad. 22: 472. 1887, pro parte (quoad col. Sargent, excl. *Coulter* 77); et in Gard. Forest 1: 232, fig. 40.

1888. — Nicholson. Suppl. Dict. Gard. 594. 1900. — Rydberg in N. Am. Fl. 22: 170. 1905. — A. H. Moore in Bailey, Stand, Cycl. Hort. 5: 2582, fig. 2905. 1915. — Standl. in Contr. U.S. Nat. Herb. 23: 311. 1922. — Rehder, Man. Cult. Trees Shrubs 280. 1927; ed. 2. 275. 1940; et Bibliogr. Cult. Trees, Shrubs 159. 1949.

Frutex usque 2.3 m. altus, ramis robustis, bienniis 3 mm. diametro, brunneis, longitudinaliter rimulosis, hornotinis 1.5 mm. diametro, dense hirsutis, pilis basi haud incrassatis, gemmis axillaribus conicis, strigosis, pilis luteis; foliis ovatis vel ovato-ellipticis, 2.5–4.5 (raro 5) cm. longis, 1–2 (raro 2.5) cm. latis, basi rotundatis, apice acutis vel obtusis, apiculatis, supra hispidis, subtus dense argenteo-villosis, 3- vel 5-nerviis, margine inconspicue serrulatis, dentibus utrinque 1 usque ad 5, minutis, petiolo 3–5 mm. longo; floribus solitariis, pedicellis brevissimis, 2–3 mm. raro ad 6 mm. longis, cum hypanthiis calycibusque dense albo-villosis; hypanthiis subglobosis, 5 mm. diametro, pilis longioribus et brevioribus intermixtis; sepalis ovatis, acuminatis, 8 mm. longis, 4–5 mm. latis; corolla usque 4.5 cm. diametro, petalis obovatis, 2 mm. longis, 1.6 cm. latis, apice erosis; staminibus ca. 40, antheris 2 mm. longis; disco medio piloso, stylo brevissimo, 1 mm. longo, stigmatibus 4 mm. longis, liberis; capsulis subglobosis, 1 cm. diametro; seminibus longe caudatis.

MEXICO: Nue vo Leon: Monterey, Sierra Madre Mts., Diente Canyon, C. H. & M. T. Mueller 544(A, F); C. G. Pringle 2094(A, NY, US); C. S. Sargent in April 1887(A TYPE; G, originally placed under *P. coulteri*); Cerro de la Silla, S. S. White 1470(G).

In the publication of *P. coulteri*, Watson cited two collections, *Coulter* 77 from Zimapan and *Sargent s.n.* from Monterey. Watson's species was published in 1887. Sargent's specimen was collected in April of that year. It is highly possible that Watson had prepared the description of *P. coulteri* before he saw the Sargent specimen. When Sargent sent him his Monterey collection, Watson simply incorporated it in his new species. As the species was named for Coulter, his collection naturally becomes the type of *P. coulteri* Wats. But Sargent's collection is definitely different from the type of *P. coulteri* Wats. which has the rugose branchlets and strigose leaves, characteristic of species like *P. mexicanus* Schlechtendal. Sargent's material has villose branchlets and leaves hispid above and densely white villose beneath, a type of pubescence characteristic to the northern element like *P. madraensis* Hemsl. Yet Sargent's specimen is not Hemsley's species because of its exposed buds, and it is thus described as new here.

Philadelphus sargentianus is endemic to Monterey where it grows at altitudes of 1500–1600 meters, where the mean annual temperature is 62°–67° F. and the mean annual rainfall is limited to 30–40 inches. There its fragrant white flowers appear from early April to July. As far as I know this species has never been introduced into cultivation. Unfortunately misled by the publication of an illustration drawn on the basis of the Sargent collection, several authors of standard references on

the cultivated trees and shrubs had misinterpreted this species as *P. coulteri*.

13. *Philadelphus pringlei*, sp. nov.

Philadelphus coulteri sensu Brandegee in Univ. Calif. Publ. Bot. 4: 270. 1912, non Wats.

Frutex, ramis brunneis, bienniis 2 mm. crassis, longitudinaliter rimulosis, hornotinis 1.5 mm. diametro, dense hirsutis, pilis basi incrassatis, gemmis axillaribus conicis, pilosis; foliis ovatis, raro lanceolatis, 2.4–5 cm. longis, 1–1.8 cm. latis, basi rotundatis, obtusis, raro acutis, inconspicue triplinerviis, apice acutis, breviter acuminatis vel raro obtusis, apiculatis, inconspicue serratis, serrulis utrinque 2 usque ad 5, minutis argutisque, supra hispidis, subtus dense argenteo-villosis, petiolo 4–5 mm. longo; floribus solitariis, pedicellis 2–4 mm. longis, cum hypanthiis calycibusque dense albo-villosis; hypanthiis subglobosis, 5 mm. diametro; sepalis ovatis, 8 mm. longis, 5 mm. latis, acuminatis; corolla cruciformi, 4–5 cm. diametro, petalis obovatis, 2 cm. longis, 1.5 cm. latis, apice rotundatis; staminibus 40 usque ad 44, antheris oblongis, 2 mm. longis; disco glabro, stylo 4 mm. longo, glabro, supra diviso, stigmatibus 3–3.5 mm. longis; capsulis subglobosis, immaturis 7 mm. diametro.

MEXICO: Nuevo Leon: Sierra Madre, above Monterey, *C. G. Pringle 10174* (A, TYPE; F, G, MO, US, ISOTYPES); Diente Canyon, about 12 miles south of Monterey, *C. H. & M. T. Mueller 261* (A, F); Waterway below Alamar, about 15 miles southwest of Galeana, *C. H. & M. T. Mueller 656* (A, F, NY).

Geographically this species has the same range as *P. sargentianus* S. Y. Hu and morphologically they are very similar except *P. sargentianus* has a pubescent disc and style, while this species has glabrous ones. According to the collectors, this taxon is abundant in the open woods and shrub zones of the Sierra Madre Oriental in the state of Nuevo Leon. Its white flowers appear in April and May.

14. *Philadelphus calcicolus*, sp. nov.

Frutex usque ad 5 m. altus, ramulis teretibus, cinereis, bienniis 1.5 mm. crassis, corticibus clausis, hornotinis brunneis, 1 mm. diametro, pilosis, gemmis terminalibus conicis, strigosis, pilis luteis; foliis serratis, lanceolatis vel ovatis, 2.5–5 cm. longis, 1–2 cm. latis, basi acutis vel obtusis, trinerviis apice subacuminatis et apiculatis vel acutis, supra in sicco nigrescentibus, pilosis, subtus olivaceis, sparsissime villosis, petiolo 5–8 mm. longo; floribus solitariis, pedicellis 3–6 mm. longis, incanis, hypanthiis subglobosis, 6 mm. diametro, dense tomentosis, argenteis; sepalis ovatis, acuminatis, 7 mm. longis, basi 4.5 mm. latis, argenteis; corolla 3 cm. diametro, petalis obovatis, apice emarginatis, 1.5 cm. longis, 1.3 cm. latis; staminibus ca. 40, antheris sagittatis, 2 mm. longis; disco glabro, stylo brevissimo, 1.5 mm. longo, stigmatibus 4 mm. longis, cristatis,

coalescentibus; capsulis ellipsoideis, 8 mm. diametro, sepalis persistentibus $\frac{1}{3}$ apicem insertis; seminibus breviter caudatis.

MEXICO: Nue vo Leon : Dulces Nombres, *F. G. Meyer & D. J. Roger* 2662 (TYPE, MO; fragment A); Canyon above Linare toward Galeana, *A. J. Sharp* 45787 (TENN, A, sterile). Tamaulipas : Road above Ciudad Victoria toward Jaumave, dry canyon slope below 3000 ft., *Sharp, Shanks, Wolfe & Hernandez* 52006, (A, TENN).

This species grows on dry limestone cliffs above a dry stream bed at an altitude of 1300 meters. The white flowers appear in June. It is a very interesting plant for most of the lateral buds on the branchlets are weak, as a rule not visible, and do not develop in the following year. Often only those situated near the apices of the shoots, either the apical alone or the two axillary ones, develop into flowering or vegetative shoots. In this respect as well as by its short styles with long cristate stigmas, emarginate petals, and slender petioles this species resembles *P. osmanthus* S. Y. Hu. The latter species can be distinguished by its pubescent disc, less canescent hypanthium and calyx, and hairs with thickened bases on the stem. Its smooth appressed white indumentum on the hypanthium and calyx and its hairs on the stem not thickened at the base also suggest a relationship with *P. argenteus* Rydb., in the section *Microphyllus* of the subgenus *Euphiladelphus*. Rydberg's species can be distinguished by the enclosed buds and small entire leaves which are densely white pubescent beneath. The coalescent stigmas and the short caudate seeds also suggest some relationship with the southern Appalachian species *P. hirsutus* Nutt., but the latter species can be distinguished by its prominent axillary buds, the style longer than the stigmatic column, and the ecaudate seeds.

(To be concluded)

POLYPLOIDY AND APOMIXIS IN COTONEASTER

HALLY J. SAX

THE ROSACEAE have drawn the attention of investigators because of the variety and beauty of their flowers and fruits as well as their horticultural value. They are a large and varied family with a wide distribution. Many examples of polyploidy and apomixis have been reported in this family.

Of the four subfamilies of the Rosaceae, the Pomoideae are of special interest because of their allopolyploid origin. The basic chromosome numbers of the other subfamilies, the Rosoideae, Prunoideae and Spiroroideae, are 7, 8, and 9. The basic chromosome number of the Pomoideae is 17, derived from primitive ancestors by hybridization followed by chromosome doubling.

The eighteen genera of the Pomoideae are rather closely related, as is shown by the fact that many generic hybrids occur in nature. Their close relationships are further supported by the readiness with which most of the genera can be intergrafted.

Many of the genera of the Pomoideae are characterized by secondary polyploidy, that is, the chromosome number in many cases has doubled again, this time probably by autopolyploidy. Secondary polyploidy is common in *Malus* and *Crataegus*.

The genus *Cotoneaster* is less well known than *Malus* and *Crataegus* of the same subfamily. In his "Manual of Cultivated Trees and Shrubs" Rehder (56) notes that there are about 50 species of *Cotoneaster* in the temperate regions of Europe, N. Africa and Asia (except Japan, where there are no native species). These are mostly shrubs, rarely small trees, with some beautiful prostrate forms among them. Their fruit is especially attractive: red, black, purple and a few orange pomes. They are planted often because of their brightly colored fruits as well as the flowers, which are in many cases small, white to pinkish and of many-flowered corymbs. There are also some evergreen and partly evergreen varieties, both upright and prostrate forms, which are very beautiful with the brilliantly colored fruit.

Plant collectors have brought many species of these Cotoneasters into cultivation. Their size, variety, and adaptive qualities make them desirable as ornamental plants. The relationship of these species is not very easily determined, and the Cotoneasters have been considered a difficult genus by the taxonomist.

The characteristics often show differences in size, hairiness, etc., but mostly intensification of some character predominating over that in another species, and often that is the only difference. In reading over the descriptions of the many species and varieties, as well as observing them

in the field, it becomes apparent why *Cotoneaster* is a difficult genus for the taxonomist. In describing *C. francheti* var. *sterneana*, W. B. Turrill (74) in 1950 remarks, "While we have not sufficient information to give full reason for this, since we do not know how far hybridization happens in the wild, how plastic are individual plants, or how much intraspecific genetic variations occur, there results frequent difference of opinion between 'lumpers' and 'splitters.' Splitters have been carried too much." He cites *Crataegus* and appeals to the cytogeneticist to study *Cotoneaster*.

POLYPLOIDY AND APOMIXIS IN THE ROSACEAE

Doubling of the chromosome number at the time of union of the egg and male nuclei followed by a reduction to half the number at the time the spore mother cells divide to form the megaspores and microspores is general throughout the plant kingdom. Asexual methods, such as root or stem cuttings, leaf and axillary bulbs, budding, etc., also occur, but these do not involve a doubling and reduction of the chromosome number; the offshoot carries the chromosome number of the organ from which it comes, while in sexual reproduction there is an alternating cycle between the haploid and the diploid number of chromosomes.

Many instances of changes, modifications of the usual behavior, or abnormalities have been found to occur in the development of the egg and male nuclei and in the development of the spores to form the gametophytes which produce the eggs and the male nuclei. Some of these, such as the functioning of a cell or cells of the integument of the ovary to form the embryo, or the direct development of a megaspore mother cell without reduction to form the spores, the development of an unreduced egg cell, do not involve a change in the chromosome number. These various substitutions for fertilization and meiosis are classified under the term apomixis. Parthenogenesis, apospory, apogamy, and vegetative buds are all included.

No attempt will be made to review all the literature on the subject of apomixis. The earlier work has been reviewed by several investigators, Ernst, 1918 (16) and others including Rosenberg (58) in 1930, who gave a summary of the work up to that time. Steil in 1939 (70) reviewed the literature on ferns. Then Stebbins (68) brought the review up to 1941 in his discussion on "Apomixis in the Angiosperms." The subject again underwent a thorough review by Gustafsson (31) in 1947. Subsequently many instances of apomixis have been reported, especially in connection with polyploidy. This work, as well as the extensive literature on polyploidy, will be discussed here only in connection with the work on the Rosaceae, of which *Cotoneaster* is a member.

The role of polyploidy and apomixis in speciation, evolution and geographical distribution is well illustrated in many genera of the Rosaceae. In general there is much variation in the appearance of apomixis and a relatively high frequency of polyploidy.

Much of the early work on polyploidy in relation to speciation was done

with the genus *Rosa* by Blackburn and Harrison (4) in 1921, Täckhohn (71) in 1922, and Hurst (36, 37, 38) in 1925, 1928, and 1932. A wide range of polyploidy was found, and Hurst attempted to classify the species of *Rosa* into five basic genomes. Crosses between the basic diploid species gave rise to the complexities of the polyploid species. Later cytological studies of this same group by Gustafsson and Häkansson (32) and Gustafsson (29) gave further information indicating that the cytogenetic relationships of the *Rosa* species are more complex with both auto- and allopolyploid as well as intermediate complexes. Fagerlind (18, 20) goes even further and suggests that segmental interchange between the chromosomes of the basic genomes leads to complex pairing relationships in triploids. Both Gustafsson and Fagerlind concluded that apomixis in *Rosa* was a species trait present in diploid species, and that the present association between polyploidy and apomixis is secondary.

Many of the North American species of *Rubus* were found to hybridize by Brainerd and Peiterson (5) in 1920 and Peiterson (52) in 1921. In the experiments, hybrids between different sexual species of *Rubus* (Peiterson, 52) and other genera have in no instances shown any clear indication of apomictic reproduction, even though the parental species are closely related to apomictic forms. Longley (43) in 1924 suggested that apomictic forms existed. In 1930 Gustafsson (25) reported unreduced pseudogamy in a species of *Rubus*. In some cases of pseudogamy the number of apomictic and sexual offspring vary according to the chromosome number of the pollen parent. Darrow and Waldo (11) 1933, reported that the fertilization of a tetraploid species of *Rubus* with pollen from a diploid species yielded a majority of sexual offspring; but it and other tetraploid apomicts produced few or none with pollen from tetraploid species. Crane (7) obtained similar results when using pollen from a diploid form of *R. idaeus* on an octaploid species of *R. vitifolius*; only pentaploid hybrids were produced. When he used pollen from the tetraploid form of the same parent, hybrids and matriclinous octoploid offspring resulted. Pollen from the hexaploid *R. loganobaccus* ($2n = 42$) produced only hybrids. Petrov (53), using pollen of the hexaploid *R. loganobaccus* on a triploid with unreduced eggs, obtained hexaploid hybrids; but using pollen of a triploid, *R. idaeus*, only triploid pseudogamous progeny result.

Although polyploidy is common in the genus *Rubus*, Gustafsson (27, 28) found apomixis was confined to only one section. As in *Rosa*, many of the species are facultative apomicts.

Many of the facultative apomicts are heterozygous, and Haskell (34), 1953, has suggested that another factor in the variation of *Rubus* may be crossing over at meiosis in the production of an unreduced egg cell. In *Rubus* crosses between two facultative apomicts give sexual progeny.

The genus *Potentilla* has also provided evidence regarding the role of polyploidy in evolution and speciation (Claussen, Keck and Hiesey 6), 1940, and the role of apomixis. *Potentilla* species (Müntzing 46 and 47) showed variation in the development of the microspore mother cell. Meio-

sis was regular in the microspore mother cell of *P. argentea* but irregular in *P. collina* and *P. hirta*. *Potentilla argentea* is apomictic through facultative apospory. The embryo may develop autonomously. Similar results were reported by Popoff (55), Gentcheff (23) and Gentcheff and Gustafsson (24). The genetic studies of Müntzing and Müntzing (49) on reproduction between sexual and apomictic forms indicate that apomixis is controlled by multiple factors.

Among the Prunoideae the genus *Prunus* has been studied extensively. Meurman (45) in 1929 reported a high polyploid species, *Prunus laurocerasus* L. with eighty-eight chromosomes. Polyploidy is common in *Prunus*, and the allopolyploid origin of *P. domestica* was determined by Rybin (59) in 1936. According to Almeida (1), *P. lusitanica* is an octopolyploid with $2n = 64$, an allopolyploid of ancient origin behaving like a diploid. Cytological work by Schelhorn (65) showed great irregularity in the nuclear divisions and tetrad formation in a triploid of *P. avium*, which the author believes arose by the fertilization of an unreduced sexual cell of *P. avium* with a sexual cell, and not as a cross of *P. avium* and *P. cerasus*.

The basic diploids show considerable stability of the genome, as is evidenced by the regular meiosis and high fertility of the hybrid between *P. tomentosa* from China and *P. besseyi* from Central North America (Sax unpublished). Apomixis has not been found in this subfamily.

Little cytological work has been done on the Spiroideae, but both autopolyploidy and allopolyploidy have been found in *Spiraea*, Sax (64). Polyploidy appears to be related to geographical distribution, since the Old-World species are largely diploid while most of the American species are late-flowering tetraploids.

The Pomoideae are unique in that the subfamily is of allopolyploid origin. Secondary polyploidy is common in most of the genera, and triploids play an important role in both natural and cultivated species. Polyploidy has complicated the genetic and taxonomic variation of most of the genera and in a few cases is related to geographic distribution.

The first extensive work on the genera of Pomoideae was done by Longley (42) in 1924. He determined the chromosome number in eighty species of *Crataegus* from the collection in the Arnold Arboretum. He found thirteen diploids, sixty-seven triploids, and ten tetraploids.

The chromosome relationship in the Pomoideae was studied by Sax (62 and 63). In the Rosaceae the subfamilies, the Rosoideae, Prunoideae and Spiroideae, have basic chromosome numbers 7, 8 and 9, while the Pomoideae have 17 as the basic chromosome number. The close relationship among them suggests that they originated as a cross between primitive ancestors of the other Rosaceae.

Dermen (12) in 1936 discovered in *Malus hupehensis* a delayed development of the embryo from the unreduced egg after the flower opened.

Johansson (39) suggested that there were four places of fruit origin: the Caucasian region, the Turkestan region, the East Asiatic region in-

cluding East Siberia, and North America. The new varieties arose through crossing, mutation, and doubling of the chromosome number.

Polyploidy in *Malus* has been studied by several workers. Einset (13, 14) found spontaneous polyploids among apple seedlings. Einset and Inhofa (15) also described periclinal chimeras; partly diploid, partly tetraploid, in apples. Hemming (35) discusses the origin of apples and the relation of diploid, triploid, and tetraploid species.

Some correlation has been shown between geographical distribution and polyploidy. Hägerup (33) in 1931 postulated an increase in the frequency of polyploidy with the increase in latitude. The results of studies by Tischler (73) of the frequency of polyploids at different latitudes in Sicily, Schleswig-Holstein, the Faeroes and Iceland supported that hypothesis. Further corroboration came from Flovik (22) in his investigations of the flora of Spitzbergen, all glacial survivors.

Gustafsson (26), Babcock and Stebbins (2), and Stebbins and Babcock (67) have found apomicts to be excellent material for studying the effect of environment on the genotype and the tracing of plant migrations. The distributional center of the American *Crepis* complex was found in northeastern California. Fernald (21), followed by Babcock and Stebbins (2), also considered the Appalachians to hold the ancient American *Antennaria* complex. Gustafsson (28) has made similar studies of *Taraxacum* and *Rubus* in Scandinavia. Curtis (9) also used apomicts in *Taraxacum* in England for the study of the effect of environment on the genotype.

Other literature on the subject of plant distribution was reviewed by Löve and Löve (44) in their work on "The Geographical Significance of Polyploidy." They conclude that polyploidy increases with the increase in latitude or the extremeness of the Pleistocene or post-glacial climate. The estimated frequency of polyploidy in the temperate zone is 30 per cent or lower.

COTONEASTER

In the present work the chromosome numbers of most of the species in the genus *Cotoneaster* were studied. It was hoped that this would show something concerning the relationships of some of the species, whether or not the species were polyploid, and give evidence as to whether there existed in this genus some of the irregularities in reproduction found in other genera of the Rosaceae as in *Malus* and *Crataegus*.

The presence of apomixis was also tested. Each season the flowers on some of the branches of a few species were destyled and emasculated while in the bud on some of the plants to see if they would produce fruit without fertilization; and if, as has been found in the apples, the development of the embryo could take place independently of fertilization by development from some part of the ovule. There are only a few species in which this work was done. Since only positive results were conclusive because in a few cases no fruit was set on the controls or occasionally on the entire plant, these results will be mentioned in connection with the species.

Seed from some of the species were planted to compare the progeny from the same seed source, to observe their resemblance to the parent plant, and to determine the proportion of hybrid plants occurring in natural populations.

The Cotoneasters in the Arnold Arboretum are all introduced species from Europe, Asia, and Africa. A few of these species were obtained from crosses made in cultivation; others were collected and brought into cultivation. The source of the species was usually known, especially the immediate place from which it was introduced. In most cases the plants came directly from their place of origin. The Arnold Arboretum's own collector, Ernest Wilson (75) brought seeds and plants from Asia directly to the Arnold Arboretum. Many of them bear the authority of Rehder and Wilson. In other cases seeds have come from well-known plant explorers in England, France, Germany, Holland, China, and India, and other equally familiar sources elsewhere and in the United States.

The material for the present work was collected during the spring and summer of the years 1950 through 1954 and was confined to the species available in the Arnold Arboretum. This included most of the well-known species, as may be noted from the list given in the table (Table I), although not all the varieties of each species were studied. There were a few plants labeled "C. sp." denoting the difficulty in naming them, and as mistakes in labeling may occur in the best collections, the number on the metal label on each specimen was copied for further tracing if necessary. All were checked with the specimens in the herbarium of the Arnold Arboretum.

The Cotoneasters blossom over a fairly long period in the spring, but it is necessary to obtain the dividing microspore mother cells at the right stages in division. During a particularly warm day most of the buds on a plant might pass through the division stages. In some species where new buds are produced over a longer period, material is more easily obtained. The difficulties of fixing such a large number of varieties in a short time meant that some were missed some years. In some rare cases the plants were not in flower every year or they were newly planted. The size of the flower bud when the divisions occurred differed in the various species. However, most of the available species, though not all, were obtained when the divisions were in progress each season, and the results were determined and checked. All those reported were checked at least two seasons, and many were studied four or five seasons.

The buds were fixed in alcohol acetic solution twenty-four hours, then changed to 95% alcohol. These were left under refrigeration until acetocarmine smears of the pollen mother cells could be made and studied.

The chromosomes in the Cotoneasters are small, but there was an abundance of material and in practically all cases it was possible to obtain well-fixed material at all stages.

In the study of the chromosome numbers it was noticeable that the chromosome pairing was quite characteristic for any given species. In many of the species there was a tendency for the sets of chromosomes to

adhere strongly in the late prophase and metaphase, and at these stages in many cases the count would be 17 or thereabout even when the form was triploid or tetraploid except for a few univalents. The chromosomes in these cases would appear unusually large for *Cotoneaster*. However, as the chromosomes separated and were counted in the anaphase stage, it was apparent that the species were often triploid or even tetraploid.

The diploids are very regular in their divisions. The 17 small chromosomes pass to the poles and are easily counted. The polyploids were not so easily counted in all cases, but they had a very characteristic appearance. The chromosome complex was larger and the pollen mother cells were usually so much larger that they suggested polyploidy after one became familiar with them. This did vary somewhat, but in all the diploids studied the pollen mother cells were smaller than in most polyploids; exceptions were noted in the polyploids.

Univalents were very often present in the dividing nuclei of the polyploids. The triploids showed chromosome bridges and other irregularities. The chromosome count varied according to the closeness of adherence of homologous pairs. Often pieces of chromatin, even whole chromosome bridges were left outside in the cytoplasm. As many as twelve such chromosome remnants were counted, but usually two to six were found outside in the cytoplasm. These were visible after the daughter nuclei had rounded up in the later stages. Tetraploids were less irregular, although univalents were often present. The number was obviously larger, and when they separated the counts showed the tetraploid number. At time some of the univalents were lost in the cytoplasm.

The counting of the chromosomes in the polyploids is complicated by an early loosening of the arms of the V-shaped chromosomes as they near the poles, which makes it appear as a larger number of chromosomes if the two arms are counted separately.

In every species the counts were checked from the same slides by Professor Karl Sax, to whom I wish to express my thanks.

The results of these studies are given in Table I. The species are listed in alphabetical order.

TABLE I
COTONEASTER

Species and Variety	Habitat	Zone	Chromosome Number
<i>C. acuminata</i> Lindl. 226-39 *	Himalayas	5	2 n
<i>C. acutifolia</i> Turcz. 15686	N. China	4	2 n
<i>C. acutifolia</i> ? 2291	Tao Basin		3 n
<i>C. acutifolia</i> var. <i>villosula</i> Rehd. & Wils. 13165B	Cent. & W. China	5	4 n

* Numbers refer to Arnold Arboretum accession numbers.

Species and Variety	Habitat	Zone	Chromosome Number
<i>C. adpressa</i> Bois 7951	W. China	4	3 n
<i>C. adpressa hessei</i> 813-41			3 n
<i>C. adpressa</i> var. <i>praecox</i> (Vilm.) Bois & Berthault. 134-18			3 n
<i>C. affinis</i> var. <i>bacillaris</i> (Lindl.) Schneid. 17806-A & B	Himalayas	7	4 n
<i>C. ambigua</i> Rehd. & Wils. 134-22	W. China	5	3 n
<i>C. apiculata</i> Rehd. & Wils. 7275	W. China	4	3 n
<i>C. bullata</i> Bois 861-32A	W. China	5	3 n
<i>C. bullata</i> f. <i>floribunda</i> (Stapf) Rehd. & Wils. 6685-2	W. China		3 n
<i>C. bullata</i> var. <i>macrophylla</i> Rehd. & Wils. 13426	W. China		3 n
<i>C. conspicua</i> Marquand 1019-36C	W. China	7 ?	2 n
<i>C. dammeri</i> Schneid. 137-51	Cent. China	5 ?	2 n
<i>C. dielsiana</i> Pritz. 686-33	Cent. & W. China	5	3 n
<i>C. dielsiana</i> Pritz. 134-28A & B			3 n
<i>C. divaricata</i> Rehd. & Wils. 6587C	Cent. & W. China	5	3 n
<i>C. foveolata</i> Rehd. & Wils. 13431A & B	Cent. China	4	3 n
<i>C. francheti</i> Bois 130-32D	W. China	6 ?	4 n
<i>C. frigida</i> ? Lindl. 191-40	Himalayas	7	2 n
<i>C. froebelli</i> Vilmorin 757-30B	Cult.		3 n
<i>C. glabrata</i> Rehd. & Wils.	W. China	7	2 n
<i>C. glaucophylla</i> Franch. 571-36	W. China	7 ?	3 n
<i>C. henryana</i> Rehd. & Wils. 223-07	Cent. China	7 ?	2 n
<i>C. horizontalis</i> Decne. 45-34	W. China	4	3 n
<i>C. horizontalis</i> var. <i>perpusilla</i> Schneid. 7157A	W. China		3 n
<i>C. horizontalis</i> var. <i>prostrata</i> 1070-38			3 n
<i>C. integerrima</i> Med. 1776-3, 1766B	Europe, N. Asia to Altai	5	3 n
<i>C. lindleyi</i> Steud. 372-37-A	Himalayas	6 ?	3 n
<i>C. lucida</i> Schlecht. 3284A & B	N. China, Mongolia Altai Mts.	4	3 n
<i>C. melanocarpa</i> Lodd. 6679-1	Europe to Cent. & N.E. Asia	4	4 n
<i>C. melanocarpa</i> var. <i>commixta</i> Schneid. 656-33			4 n ?
<i>C. melanocarpa</i> var. <i>laxiflora</i> (Lindl.) Schneid. 13490-1A	Cent. Asia		3 n
<i>C. microphylla</i> Lindl. 22906	Himalayas	5	2 n
<i>C. moupinensis</i> Franch. 13497A & B	W. China	6 ?	3 n
<i>C. multiflora</i> Bge. 21976, 14916	W. China	5	4 n

Species and Variety	Habitat	Zone	Chromosome Number
<i>C. multiflora</i> var. <i>calocarpa</i> Rehd. & Wils. 6679-1 & 2	W. China		3 n ?
<i>C. multiflora</i> var. <i>granatensis</i> (Boiss.) Wenz.	Spain	6	3 n
<i>C. nitens</i> Rehd. & Wils. 6681	W. China	4	3 n
<i>C. obscura</i> Rehd. & Wils. 6686-1	W. China	5	3 n
<i>C. obscura</i> var. <i>cornifolia</i> Rehd. & Wils. 11261A & B	W. China		3 n
<i>C. racemiflora</i> var. <i>desfontaini</i> (Reg.) Zab. 389-34	S. Eur., N. Afr., W. Asia to Himalayas and Turkestan	4	3 n
<i>C. racemiflora</i> var. <i>soongorica</i> (Reg. & Herd.) Schneid. 16428, 21846	W. China	3	3 n, 4 n
<i>C. racemiflora</i> var. <i>veitchii</i> Rehd. & Wils. 20075	Cent. China		3 n
<i>C. rosea</i> Edgew. 44939	N.W. Himalayas, Afghanistan	5	3 n
<i>C. rotundifolia</i> Lindl. 405-36A	Himalayas	6 ?	3 n
<i>C. rubens</i> W. W. Sm. 21991B	W. China	6 ?	3 n
<i>C. salicifolia</i> Franch. 434-33A	W. China	6 ?	
<i>C. salicifolia</i> var. <i>rugosa</i> (Pritz.) Rehd. & Wils. 458-36-A	Cent. China	5	3 n
<i>C. schneideri</i> 574-38-B			4 n
<i>C. simonsii</i> Bak. 596-33	N.W. India, Khasia	5	3 n
<i>C. sp.</i> H. Hesse 13492			3 n
<i>C. sp.</i> 524-30A & B			3 n
<i>C. sp.</i> 114-36B	China (Lu Shan Arb.)		3 n
<i>C. tenuipes</i> Rehd. & Wils. 7276A-C	W. China	5	3 n
<i>C. tomentosa</i> (Ait.) Lindl. 23-42-4A, 13507-1	S.E. Europe, W. Asia	4	3 n
<i>C. wardii</i> W. W. Sm. 659-33	S.E. Tibet	7 ?	3 n
<i>C. zabeli</i> Schneid. 7019B	Cent. China	4	3 n
<i>C. zabeli</i> var. <i>miniata</i> Rehd. & Wils. 7343D, 156-85	China		3 n

Triploid and tetraploid *Cotoneasters* are apt to be more vigorous than the diploids — but there is much variation among these; some are less vigorous. Often the main differences given in Rehder's Manual between some of the species and varieties is in vigor, intensity of color, size of flowers, leaves and fruit, pubescence, or looseness of inflorescence. There are other differences between species, but these are much the same variations existing between known diploid and triploid or polyploid species derived from them.

Cotoneaster acuminata Wallich is one of the first species described (Flora, 1823). It is a diploid species from Zone 5 in Nepal in the

Himalayas (Table I.) A natural hybrid between this species and *C. acuminata* was collected by R. N. Parker. *Cotoneaster acuminata* is found along the Himalayas to Calcutta.

According to the table (Table I) the chromosome count for *Cotoneaster acutifolia* Turcz. is 17. The pollen mother cells were small. It is a diploid and its natural habitat is N. China. It has been found on a mountain near Peking by Bretschneider. Specimens in the herbarium from various localities in northwest China at high altitudes are labeled *C. acutifolia* Turcz. Wilson (75) says there is no typical *acutifolia* in China proper, but in Mongolia, but that there are two well-marked varieties in central and west China.

Another plant labeled *C. acutifolia* (?), carrying a different number, was grown from seed collected by Joseph F. Rock in the Tao River Basin, Kansu Province, China. It is obviously a different variety with a triploid chromosome count and lagging chromosomes. This is a triploid probably derived from *C. acutifolia* Turcz.

One of the varieties, *C. acutifolia* var. *villosula* Rehd. & Wils., is found in Central and West China. This is a polyploid and was recognized as a new variety by Rehder and Wilson (56). It is described as "densely villous beneath, somewhat larger; calyx tube more densely villous; fruit thinly pubescent." From the chromosome counts this was considered a tetraploid, although there was some irregularity.

Closely related to *C. acutifolia* Turcz. is *C. ambigua* Rehd. & Wils. from West China which, according to Rehder's Manual of Cultivated Trees and Shrubs (56), "differs chiefly in its slightly pubescent or nearly glabrous calyx tube and subglobose fruit with three to four nutlets." *Cotoneaster ambigua* is a coarser plant in general and more rigid in appearance than *C. acutifolia* Turcz. and bears a closer resemblance to *C. acutifolia* var. *villosula* Rehd. & Wils., but on comparison of the two plants side by side in the field they appeared sufficiently different to be separate species. In *Plantae Wilsonianae*, Wilson (75) makes the remark, "In speaking of *ambigua*, it is noted that all *acutifolia* like specimens are grown in the arboretum and later it may be possible to determine their relation to each other." *Cotoneaster ambigua* is a triploid. The divisions of the nucleus in the pollen mother cells are irregular with bridges still holding at anaphase and scattered univalents. The homologues show some tendency to adhere. The pollen mother cells often did not finish dividing but decomposed at some stage in their development. There was also much variation in the stages in an anther and much decomposition in the pollen mother cells. *Cotoneaster ambigua* produced fruit. The specimen in the Arnold Arboretum was heavily fruited in 1953, suggesting apomixis in such an irregular triploid.

Cotoneaster tenuipes Rehd. & Wils. is also noted as a species closely related to *C. acutifolia* Turcz. It has a very graceful fine slender development throughout and would not be mistaken for either *C. acutifolia* var. *villosula* or *C. ambigua*. It is less coarse even than the diploid species *C. acutifolia* Turcz. *Cotoneaster tenuipes* is a triploid form which has smaller

chromosomes and pollen mother cells like those of the diploid, but the chromosome number is higher than the basic number for the genus. There were chromatin bridges and fragments in the cytoplasm at anaphase. Although the pollen grains were smaller, like those of a diploid, it was obviously a triploid or aneuploid. There was little mature fruit on the plant in the years 1950–1952, but it was well fruited in 1953. It is probably apomictic.

Cotoneaster tenuipes Rehd. & Wils. grew in West China, as did *C. ambigua* Rehd. & Wils. and *C. acutifolia* var. *villosula* Rehd. & Wils., the latter extending into central China. The two former are triploids, the latter a tetraploid. They grew in Zone 5 (i.e. Rehder's Map of Climatic Zones), while *C. acutifolia* Turcz. was found in Zone 4 and in North China.

There must be some relationship between them, as they have similarities that the systematist recognizes. There is the possibility that the triploids just mentioned came from a cross in which *C. acutifolia* was one of the parents, or that the chromosome number of *C. acutifolia* had doubled in number, forming a tetraploid (var. *villosula*) and then back-crossed with *C. acutifolia* or another diploid, giving triploids. Their distribution would support this assumption.

Cotoneaster lucida Schlecht. was once labeled *C. acutifolia* Lindl. (not Turcz.). It came from the Altai Mountains in Mongolia, Zone 4 (North China). It is quite different from *C. acutifolia* Turcz. *Cotoneaster lucida* has larger glossy and lustrous leaves. It is a triploid. It may be that this species has some relationship to *C. melanocarpa* as well as *C. acutifolia*.

Cotoneaster foveolata Rehd. & Wils. is represented by two vigorous specimens in the Arboretum grown from the same collection of seeds. They are alike. *Cotoneaster foveolata* is a large stiff shrub with large leaves. It is a triploid with much irregularity in the nuclear divisions of the pollen mother cells. Pieces of chromatin are left out in the cytoplasm after the dividing nuclei are formed. *Cotoneaster foveolata* comes from central China, Zone 4.

Cotoneaster moupinensis Franch. is a large stiff shrub which, like *C. foveolata*, has a rigid appearance. Rehder describes it as "similar to *C. bullata* but with black fruit." It comes from western Szechuan, West China, at 1300–2000 m. altitude. It is common in woods and thickets. It is a triploid. Wilson comments about the series as follows: "It must be confessed, however, that there is a great similarity between all these black fruited *Cotoneasters* from China." He noted that there were only slight variations between these *acutifolia*-like species and that they could be arranged in a gradual series. He believed that since they are all cultivated in the Arnold Arboretum someone may later determine their affinities and find the relations of the *acutifolia*-like ones.

Cotoneaster bullata Bois and its variety *C. bullata* var. *macrophylla* Rehd. & Wils. are among the most attractive shrubs in the Arboretum in the autumn because of their large clusters of abundant brilliant red fruits and very healthy dark green leaves. The *macrophylla* variety is especially

striking, having a larger leaf and inflorescence. Wilson says that *C. bullata* is a comparatively rare plant, though scattered over wide areas in Szechuan. It is found in open conifer forests in southeastern Tibet at 9000–10000 feet, inhabiting Zone 5—a zone adjacent to that of *C. moupinensis*, which is in Zone 6 in that same area. *Cotoneaster bullata* Bois is a triploid. The division of the nuclei of the pollen mother cells was very irregular, with twenty-two to twenty-eight chromosomes, depending on the looseness of pairing. There were chromosome bridges and many univalents, up to as many as twelve in one anaphase.

The variety *C. bullata* var. *macrophylla* Rehd. & Wils. is also a triploid; univalents, bivalents, and trivalents are present. It is very irregular, with chromosome bridges at anaphase.

Another form, *C. bullata* f. *floribunda* (Stapf) Rehd. & Wils. is very attractive. It also has a triploid number with univalents and lagging chromosomes, but its homologues seem to be more closely paired. Under his remarks Rehder includes *C. moupinensis* var. (Stapf) as a synonym. It seems significant that this form *C. bullata* f. *floribunda* was described as *C. moupinensis* var. Stapf. It has bright red berries. *Cotoneaster bullata* f. *floribunda* is also found in the thickets of Szechuan, China. It is possible that *C. bullata* and varieties came from similar parental ancestry as *C. moupinensis*.

Very bright red berries with intensely green foliage and an attractive low habit characterize *C. apiculata* Rehd. & Wils., which grows in West China. This is a triploid with chromosome bridges and other irregularities in the reduction divisions in the anthers. In the late anaphase there are chromosome fragments left in the cytoplasm. Rehder gives *C. apiculata* as nearly related to *C. disticha* Lange, which ranges from the Himalayas to southwest China. (The latter was not in the Arboretum collection except for small cuttings, and it is not included in the counts. Counts on leaf-tip smears show that it is not a diploid.) There were three plants of *C. apiculata* grown from seed collected from the type plant by Wilson in China. They were alike. George Graves raised twenty-five plants from seed collected in the Arboretum. All were alike. The same was true of twenty-nine seedlings grown in the greenhouse, making a total of fifty-seven seedlings from the same original source.

Cotoneaster Lindleyi Steud. is a triploid. It produced no fruit 1950–1952, although it had some flowers on it in 1950 and 1951. In 1953 it flowered abundantly and produced fruit. This fruit became a deep lavender or bluish purple as it developed (much like that of *C. affinis* var. *bacillaris*) and gradually turned a purple brown and finally black—a word used by Rehder. Rehder includes *C. Lindleyi* as a species closely related to *C. racemiflora* (Desf.) K. Koch. It is a conspicuous species with its broad oval to broad ovate leaves rounded at the base. It came from the Himalayas (Rehder, Zone 6). It was very susceptible to fire blight.

Cotoneaster affinis var. *bacillaris* (Lindl.) Schneid. is probably a tetraploid. There were seventeen large tetravalent chromosomes in early equa-

torial plate stage and double that number at anaphase. Like *C. affinis* Lindl., which is not in the Arboretum, it is said by Rehder (56) to be closely related to *C. frigida*.

Cotoneaster frigida Lindl. is a diploid having seventeen chromosomes. Our specimen of *C. frigida* is quite different from the upright type described as typical. It lies flat on the ground with branches very stiff, like the one collected at Darjeeling. Some fruit set on the two destyled branches. The fruit is large and of a bright red color quite unlike that of *C. affinis bacillaris*. The latter is found in the Himalayas, as is *C. frigida*. They grow in Zone 7 (Rehder).

It is probable that *C. affinis* var. *bacillaris* came from the doubling of the chromosome number in *C. frigida* or a cross between *C. frigida* and some other form. There is quite a noticeable similarity between *C. affinis* var. *bacillaris* and *C. lindleyi*, which is a triploid. *Cotoneaster lindleyi* may have come as a backcross from *C. affinis* var. *bacillaris* and a diploid. There are several diploids in that region.

In writing of the variety *C. dielsiana* var. *elegans* Rehd. & Wils., Wilson remarks on the herbarium sheet that "this western plant shows marked differences from the type . . . in several respects approaching *francheti* Bois. It also has affinity with *C. Zabeli* Schneider. Its thinner yet more persistent leaves, smaller pendulous fruit, brick and orange red, distinguish this variety from the typical form." It is found in thickets 3500–4000 feet on the eastern slope of Likiang snow range, Yangtze Watershed, Szechuan. These observations are supported by a study of the chromosomes.

There are three specimens of *C. dielsiana* Pritz. in the Arboretum. One (*C. dielsiana* 686–33) was from the United States Department of Agriculture. After *C. dielsiana* was fixed two years in succession, a difference in the behavior of the chromosomes was noted for the two years. A check of the numbers showed that the material had come from the other two plants the second year. These two plants were grown from seeds labeled *C. dielsiana* 134–28–A & B, which were collected by Wilson in China, and they are alike. The fruit of this specimen is red and waxy and the leaves have color in the fall. It fits the description by Rehder. The fruit of the U. S. D. A. specimen is a reddish yellow fruit like that described for the variety *elegans*. *Cotoneaster dielsiana* (686–33) varied in the chromosome counts, depending on the looseness of pairing of the homologues. There were univalents, bivalents, and trivalents. Bridges were present in the anaphase stage. This is undoubtedly a triploid.

The chromosome counts from the specimens grown from the seed from China (134–28) appear to be 17 and up to about 21 in equatorial plate stage, depending on looseness of adherence. In the first anaphase the count appears to be higher than it appears at metaphase, and univalents and stragglers are apparent. The second anaphase counts are 17 and higher with irregularities. This may be an aneuploid.

George Graves grew a thousand seedlings from seed collected in the Arnold Arboretum. They were uniform in habit and growth like the 673

seedlings from 134–28 grown in the greenhouse. They are undoubtedly apomicts, as there were many kinds of *Cotoneasters* growing near by.

There were five specimens of *C. divaricata* Rehd. & Wils. growing from a collection of seeds from China. There were no discernible differences between these. George Graves grew two hundred seedlings of *C. divaricata*. They showed no variation.

Cotoneaster divaricata is a triploid species with lagging chromosomes and univalents. It is very probably an apomictic triploid.

There are several varietal forms of *C. racemiflora* (Desf.) K. Koch (in the Arnold Arboretum) which are quite widely distributed in their origins and show much variation. They are found in southern Europe, North Africa, western Asia to the Himalayas and Turkestan. *Cotoneaster racemiflora* (Desf.) K. Koch is described by Rehder (56) as "a variable species, the typical form variety *C. racemiflora* var. *desfontaini* (Reg.) Zab. (var. *typica* Schneid.) has generally elliptic acutish leaves, while variety *nummularia* Dipp. has broader usually obtuse leaves."

The divisions of the nucleus of the pollen mother cells in *C. racemiflora* var. *desfontaini* (Reg.) Zab. are fairly stable in appearance, but there are some univalents and bridges in both divisions and some chromatin left out after the daughter nuclei are formed. The pollen mother cells and the chromosomes are large for the genus and the chromosome count shows that it is polyploid, probably a triploid, the homologues pairing loosely.

Some fruit set on the destyled pistils in *C. racemiflora* var. *desfontaini*, but only on some of the destyled branches. However, when set, the fruit was abundant on the destyled branches as well as on the controls.

Cotoneaster racemiflora var. *soongorica* (Reg. & Herd.) Schneid. from West China is represented in the Arboretum by two plants from different sources. They are growing side by side. The fruit of one, which came from the Framingham Nurseries, is a little darker in color, maturing a little later than the other, which was grown from seed (Hort. Judd). They both appear to be triploids, but there are some differences in their chromosome behavior. In the plant raised from seed there appeared to be a higher chromosome number. Perhaps the homologues were more easily separated. One of the obvious phenomena noticed in both cases — but especially in the plant from the nursery — was the large number of examples of the stages where the homologues were pulled apart along the plate but still adhering. The whole complex would be in that condition with several univalents and bivalents less regularly placed.

Cotoneaster racemiflora var. *veitchii* Rehd. & Wils. from Central China possessed the number of chromosomes and the irregularities of a triploid.

Cotoneaster rosea, another triploid, has attractive small pink flowers in glabrous three- to nine-flowered cymes. It comes from the northwestern Himalayas and Afghanistan. It is probably a facultative apomict, as it hybridizes at times with *C. acuminata*, according to Parker's notes on the herbarium sheet. Its branches are slender. It is supposed to be related to *C. racemiflora*, as shown especially by its fruit.

Cotoneaster multiflora Bge. is a very graceful shrub from western

Szechuan. It is handsome in bloom and it has attractive red fruits. This is a tetraploid. The counts are around 34. Late anaphase shows a larger count, which is characteristic, as the two arms of the chromosome separate further in the reorganization of the daughter nuclei. The divisions are fairly regular. Although *C. multiflora* grows in West China, the Arnold Arboretum Herbarium has also a specimen from Kashmir. This may be a variety of *C. multiflora* or of *C. racemiflora*.

Cotoneaster multiflora var. *calocarpa* Rehd. & Wils., with rosy-colored blossoms, shows much irregularity. It is probably a triploid, although at times it appeared to have too many chromosomes. They may be the homologues prematurely separated.

Cotoneaster multiflora var. *granatensis* (Bois.) Wenz. is a triploid, the chromosome counts varying with many univalents — as many as fifteen in one case. The homologues varied in the ease with which they separated. In some cases the division went no further than the pollen mother cells. There was much sterility. The pollen mother cells, as well as the chromosomes, were large.

Among the unidentified species *Cotoneaster* sp. Hesse 13492G is a triploid. The two unnamed specimens collected by Dr. Rock are also triploids. They are alike and came from the same collection of seeds.

It was found that two collections labeled *C. obscura* and collected at different times yielded different results as far as behavior of chromosomes was concerned. One of these gave results similar to those obtained from the material labeled *C. obscura* var. *cornifolia*. A survey of these specimens in the field showed the two latter to be similar, and a checking of the numbers carried by these shrubs against the cards in the files disclosed that the plants had come from the same collection of seeds! (The large label on the questionable plant had omitted the varietal name.) *Cotoneaster obscura* var. *cornifolia* Rehd. & Wils. is a triploid, as it is very irregular with univalents, lagging chromosomes, and irregular pollen size. *Cotoneaster obscura* is also a triploid, but it has fewer chromosomes and is somewhat less irregular in its divisions. The homologues may adhere more closely or it may be an aneuploid. It is not as coarse in general, having smaller leaves, more delicate branches, and dark red fruit, while the variety *cornifolia* has a purple-black fruit. These are both from West China. They are probably apomictic triploids related to *C. acutifolia* or a cross between *C. acutifolia* var. *villosula* and some diploid.

Cotoneaster francheti Bois and *C. schneideri* appear to be identical or nearly so. The appearance and behavior of the chromosomes first called my attention to the similarity. When the plants were checked in the field, they were almost identical. The red fruit of *C. francheti* Bois was a bit more deeply colored than that in *C. schneideri* which was orange-red. The latter, however, although located near by, is more shaded by other plants. It could, of course, be an apomict which is a "clonal variety" with very slight differences. Rehder (56) does not mention *C. schneideri*. The plant in the Arnold Arboretum came as seed from California. *Cotoneaster francheti* is a tetraploid species. It comes from West China.

Rehder comments on the similarity between *C. francheti* Bois. and *C. wardii* W. W. Sm. The leaves of *C. wardii* are larger and in general the bush is more vigorous. It looks quite different. The fruit is larger and red without the orange-red tint noticeable in the red of *C. francheti*. The chromosome behavior is different. *Cotoneaster wardii* is a triploid, probably with *C. francheti* as a parent. This may be a case where the triploid is more pronounced in various ways than the tetraploid.

Two plants of *C. simonsii* in the Arboretum come from different sources; one from seed from Wageningen, Holland, the other as a plant from a nursery. They are not exactly alike in chromosome behavior, one being more irregular with long bridges stretching from pole to pole in the anaphase and with many univalents. The other is a little less irregular, but the chromosome count is the same. Both are triploids according to chromosome count and behavior. The plants vary somewhat, too. The fruits of one are almost always solitary or in a small cyme; the other fruits are in a cyme. The one with solitary fruits is much like the variety *newryensis*, nearly related to *C. francheti*. A total of 384 seedlings of *C. simonsii* gave three variants.

Cotoneaster zabeli Schneid. is represented by four specimens — all from the same collection of seeds. They are alike. *Cotoneaster zabeli* is a triploid. In the third year of the experiment fruit was borne on the destyled branch.

Cotoneaster zabeli var. *miniata* Rehd. & Wils. is a smaller, more delicate variety in habit and flower, with a light orange-scarlet fruit instead of the bright red borne by *C. zabeli*. It is also a triploid. This, like *C. tenuipes*, was expected to be a diploid. It may be an aneuploid, as the count is low for a triploid.

Cotoneaster tomentosa (Ait.) Lindl. is represented by two plants in the Arboretum. They are alike. Each year the flowers on several branches were destyled while in the bud. These set fruit in about the same proportion as on the controls. Apomixis is very definitely shown here. These plants continue to flower all summer up to frost time; only a few flowers are in blossom on each branch at a time. *Cotoneaster tomentosa* is a triploid.

Rehder (56) speaks of *C. tomentosa* being similar to *C. integerrima*, but larger in every part and more pubescent. *Cotoneaster tomentosa* is distributed throughout Europe and West Asia in Zone 4 (Rehder).

One specimen is reported from Kansu, but it may differ and should be compared, as no other report of that kind is made. Two new specimens from a nursery labeled *C. tomentosa* are not like the older *C. tomentosa* planted here, but are more like *C. integerrima*, but larger.

It was noted above that two plants of *C. obscura* var. *cornifolia* Rehd. & Wils. coming from the same seed source were alike in every way, the chromosomes being similar in number and appearance. Several other groups of two or more specimens from the same collection of seeds from a species were growing in the Arboretum. In all these cases plants from the same seed sources were alike. The number was not large enough in

each case to be certain if this was always true for these species, but *Cotoneasters* in general were considered to come true from seeds.

In the behavior of the chromosomes definite groupings are suggested, and a few of these species are very close together. For instance, *C. francheti* and *C. schneideri* are similar, as are the two so closely related soongoricas. A note with one specimen of *C. francheti* in the cultivated group describes the fruit as orange-scarlet. Schneider collected an orange-scarlet-fruited specimen at Gotha. Perhaps this is where the name *C. schneideri* became attached to and substituted for *C. francheti* for the California plant, as *C. schneideri* does show a slightly more orange tint. At any rate, *C. francheti* is a tetraploid which shows a deep orange red as it is ripening, and only a slight variation could be the cause of the differences in both cases. *Cotoneaster wardii*, a related triploid, lacks the orange tint altogether. *Cotoneaster francheti* is a tetraploid, which explains to some extent the "splitters" that Turrill mentions in connection with the variety "*sterniana*" and which turns up in *C. schneideri*. Crosses with other species may help to produce the triploids found in cases like *C. wardii*, *C. nitens*, *C. divaricata*, and others.

REPRODUCTION IN COTONEASTER

Most of the *Cotoneasters* have long been known to breed true from seeds. This has been shown by the uniformity in the seedlings grown from the collections of Wilson and others, and frequent mention of the fact that certain species of *Cotoneaster* could be propagated by seeds. Saunders (60), in *Refugium Botanicum*, mentions that *C. buxifolia* comes true from seeds, and gives a list of *Cotoneasters* that may be propagated by seeds. Conrad Loddiges & Sons (41) describe *C. affinis* and *C. melanocarpa* as raised from seeds. According to Stapf's (66) description of *C. bullata* in the *Botanical Magazine*, 1909, it produces an abundant crop of seeds to increase the plant.

In the literature on *Cotoneaster* several cases of natural crosses have been reported. *Cotoneaster frigida* Lindl. is of interest in this respect. It has been mentioned as one of the parents in several instances.

Exell (17) collected seeds from a plant of *C. frigida* growing in close proximity to other species of *Cotoneaster* and planted them. Among the resulting seedlings there were six hybrids; the remaining plants were like *C. frigida*. *Cotoneaster watereri* Exell was considered an interesting hybrid between *C. frigida* Lindl. and *C. henryana* Rehd. & Wils. (*C. rugosa* Pritzl and Diels.). *Cotoneaster frigida* Lindl. and *C. pannosa* Franch. gave rise to *C. crispui* Exell. The others were not of horticultural interest.

A. A. Pettigrew (54) of Cardiff obtained seeds of a *C. frigida fructiluteo* plant from Stevenstone, Devonshire. This plant differed from the type in color of the fruit only, which was yellowish or creamy white instead of red. After several years of genetic experiments, on which the final report was not available, the author found red to be dominant, and

he believed that the individual plants of *C. frigida* were self-sterile and that they were fertilized by a red-fruited variety growing in the vicinity.

Conrad Loddiges & Sons (41), in describing *C. frigida*, mention that it should be budded on white thorn stock.

Another instance of the tendency of *C. frigida* to hybridize is the announcement, in Gardeners' Chronicle 132: 243, of *C. cornubia* — a hybrid between *C. frigida* and an unrecorded species — as a vigorous plant by Mr. Lionel de Rothschild in 1933. This received an award of merit.

Others report *C. frigida* as breeding true. A. T. Johnson (40) describes *C. frigida* as naturally a free and robust tree "so readily raised from seeds." He also mentions the distinct form *fructo-luteo*. Four seedlings of *C. frigida montana* grown from seed obtained by Donald Wyman from North Africa were alike.

On a note with a specimen from the Flora of Chumbi in the Arnold Arboretum Herbarium, mention is made of the fact that seedlings of *C. frigida* Lindl. are alike; also that seedlings of *C. aldenhamensis* are all alike but not so broad-leaved as those of *frigida*.

R. N. Parker, while collecting in Khadrula India Sikkum, Himalayas, at an altitude of 2700 meters, June 18, 1928, found in a thicket a specimen which he considered a cross (*C. acuminata* Lindl. and *C. rosea* Edgew.). There is a specimen of this in the Arnold Arboretum Herbarium. This has the habit of *C. acuminata* and the pink flowers of *C. rosea*. A plant of *C. rosea* was growing near by the thicket of *C. acuminata* where this hybrid plant was found.

Caution against raising plants from seeds comes from several sources, concerning both the *microphylla* and *salicifolia* groups. Of the probable hybridization in the several species allied to *C. microphylla*, *C. congesta* (Syn. *C. microphylla* var. *gracilis*), and *C. thymifolia* Arthur Osborn (51) writes, "It is best to propagate these distinct forms by cuttings or layers. They do not come true. At least that is our experience at Kew, though this may be due to cross pollination as all are growing in close proximity." W. J. Bean (3) made similar observations, as was noted earlier. The group of species, all natives of the upper and middle basin of the Yangtze River, in which are included *C. salicifolia* and its varieties, *C. glabrata*, *C. henryana*, and *C. rhytidophylla*, have also been reported (66) to hybridize easily. *Cotoneaster watereri* is supposed to have one parent in this group.

The instances of hybridization are few and limited to species or groups where few specific data are available. In an isolated population a species would be expected to breed true, but when numerous species are growing in close proximity variation would be expected. Some cases have been cited where a small number of offspring from the same seed source are alike when species overlap and hybridization could result. The most critical test, however, is the study of the progeny of species grown in a botanical garden where many species are grown in close proximity.

In the Arnold Arboretum most of the species are grown in close proximity, and the time of flowering is essentially the same in some species

and overlapping in others. There is ample opportunity for cross-pollination, since the bees at blossoming time are so abundant that it is difficult to work with the plants.

In order to determine whether most of the species breed true from seeds where there was so much chance of cross-pollination, seeds were collected from the following species, stratified, and grown in the greenhouse: *C. acuminata*, *C. acutifolia* var. *villosula*, *C. adpressa*, *C. adpressa hessei*, *C. adpressa* var. *praecox*, *C. ambigua*, *C. apiculata*, *C. bullata*, *C. bullata* f. *floribunda*, *C. dielsiana*, *C. divaricata*, *C. foveolata*, *C. frigida*, *C. horizontalis*, *C. integerrima*, *C. lindleyi*, *C. lucida*, *C. microphylla*, *C. moupinensis*, *C. nitens*, *C. obscura cornifolia*, *C. racemiflora* var. *desfontaini*, *C. racemiflora* var. *soongorica*, *C. racemiflora* var. *veitchii*, *C. rosea*, *C. simonsii*, *C. s.* var. *newryensis*, *C. tomentosa* and *C. wardii*.

In connection with this part of the work I wish to thank Dr. Karl Sax, who helped collect the seeds, and Mr. Lewis Lipp, Jeanette Renshaw and Dorothy Thorndyke for growing and caring for the seedlings. I thank George Graves, who grew additional seedlings from three of the same seed sources and furnished the data that are also included in the table (Table II). These include 25 seedlings of *C. apiculata*, 1000 of *C. dielsiana*, and 200 of *C. divaricata*.

TABLE II
APOMIXIS IN COTONEASTER

Species	Chromosome Number	Number of Seedlings	Number of Maternals	Number of Variants
<i>C. acuminata</i>	2 n	11	4	7
<i>C. acutifolia</i> var. <i>villosula</i>	4 n	14	12	2
<i>C. adpressa</i>	3 n	6	6	0
<i>C. adpressa hessei</i>	3 n	10	10	0
<i>C. adpressa</i> var. <i>praecox</i>	3 n	4	4	0
<i>C. ambigua</i>	3 n	50	50	0
<i>C. apiculata</i>	3 n	54	54	0
<i>C. bullata</i>	3 n	14	14	0
<i>C. bullata</i> f. <i>floribunda</i>	3 n	34	34	0
<i>C. dielsiana</i>	3 n	1673	1673	0
<i>C. divaricata</i>	3 n	200	200	0
<i>C. frigida</i>	2 n	2	0	2
<i>C. horizontalis</i>	3 n	5	5	0
<i>C. integerrima</i>	3 n	44	44	0
<i>C. lindleyi</i>	3 n	16	16	0
<i>C. moupinensis</i>	3 n	21	21	0
<i>C. multiflora</i>	4 n	57	57	0
<i>C. nitens</i>	3 n	26	26	0
<i>C. obscura</i> var. <i>cornifolia</i>	3 n	16	16	0
<i>C. racemiflora</i> var. <i>veitchii</i>	3 n	13	13	0
<i>C. rosea</i>	3 n	27	27	0
<i>C. simonsii</i>	3 n	384	381	3
<i>C. wardii</i>	3 n	36	35	1

The data for this work are given in Table II. In most instances the number of seedlings from each species was not large, but most of the offsprings were like the seed parent; most were maternals.

Cotoneaster acuminata and *C. frigida* showed a tendency to hybridize. They showed considerable variation in their respective progeny. Both are diploids.

The large majority of the Cotoneasters breed true. Several others did show a small percentage of variants.

Among the triploids, three of those propagated threw a small percentage of variants (Table II). Of the 26 seedlings of *C. nitens*, three were different and varying among themselves; the others were alike. One of the thirty-six seedlings of *C. wardii* varied from the type. Of 384 seedlings of *C. simonsii* all were uniform, with three exceptions. As was also true of the aberrants in *C. nitens* and *C. wardii*, the three seedlings of *C. simonsii* were conspicuously different from the others of the same species. They were striking among an otherwise uniform population. They had broader leaves which were thicker and tomentose and flattened into a rosette.

This may indicate that although *C. nitens*, *C. simonsii*, and *C. wardii* reproduced apomictically, the egg is fertilized at least at times, and that they may be crossed with other species. They are probably facultative apomictic species, as *Malus sargentii* is among the apples.

On the triploid *C. tomentosa* (Ait.) Lindl. destyled ovaries developed in about the same proportion as on the controls on other branches of the same shrub. This was also true of the destyled ovaries of the triploids *C. dielsiana* Pritz., *C. nitens* Rehd. & Wils., *C. froebellii* — a plant from Vilmorin — and *C. zabeli* Schneid., but further work along this line would be necessary before settling this point on these grounds, except for a few species. Many species so treated gave negative results, but most of the negative results are not conclusive, either because not enough work was done, or because injury in the process might cause the fruit to drop (as happened most often the first year) or because no fruit was set on the controls at the same time.

Apomixis must be very general among the triploid Cotoneasters. Many species grown in the same vicinity are in bloom at the same time. The bees and other insects are attracted to them in such large numbers that cross-pollination should be the rule. Although the divisions in the pollen mother cells were very irregular in the triploids, and often with the loss of chromatin, there was an abundant production of fruit and a great uniformity among the progeny where they were tested. This seems to establish rather definitely the presence of apomixis in the triploids.

The tetraploids were more regular in the divisions in their pollen mother cells. Seedlings of only two tetraploids, *C. acutifolia* var. *villosula* and *C. multiflora*, were grown. Among fourteen seedlings of the former two variants appeared. All were uniform in *C. multiflora*. Abundant fruit set on the plant, which was in the midst of many other species.

There is no doubt about apomixis in the triploid Cotoneasters, and it

is possible that it may exist in some of the diploids and tetraploids. There is also some evidence that some of the triploids are facultative apomicts, since three produced a small percentage of variant seedlings. It is possible that variants in other triploid species might be found if larger numbers of progeny were grown or if the triploids were hand-pollinated with pollen from triploids.

The meagre evidence of facultative apomixis in *Cotoneaster* is supported by the breeding behavior of the closely related genus *Malus*. *Malus sargentii* is found in diploid, triploid, and tetraploid forms (K. Sax unpublished). When open pollinated all produce only maternal progeny, even though they are surrounded by other species. When artificially pollinated with pollen from other diploid species, the triploids and tetraploid *M. sargentii* forms do produce some sexual progeny, but seldom more than twenty per cent. In some cases only maternal types of progeny are produced, and in all cases these types are predominant. The mechanism of this facultative apomixis is unknown. A few triploid species of *Malus* do produce an occasional variant when open pollinated, even though the great majority of the progeny are maternals. It is possible that the same type of apomixis is present in *Cotoneaster*.

DISTRIBUTION AND RELATIONSHIPS

The geographical distribution of *Cotoneaster* in relation to the 2 n, 3 n, and 4 n chromosome numbers may offer suggestions as to the origin of some of the species. Eight of the species studied are diploids. There may be other diploids among those in which the chromosome number has not been determined. The diploids *C. frigida*, *C. microphylla*, and *C. acuminata* are found in the Himalayas; *C. conspicua* in Tibet; *C. glabrata* and *C. henryana* in the Yangtze basin in western and central China; *C. dammeri* in West Hupeh in central China; and only one, *C. acutifolia* Turcz., in North China and Mongolia.

The diploids have a limited geographical distribution, and fifty per cent of them are found in Zone 7 (Rehder); only one, *C. acutifolia* Turcz., inhabits Zone 4. Wilson (75) comments that *C. acutifolia* Turcz. was originally described from Chinese Mongolia, that it was introduced by Dr. Bretschneider from mountains near Peking, and that the typical form is absent from central and western China, but varieties are found growing in these regions.

There were a number of instances in which specimens were labeled *C. acutifolia* or a variety thereof. Some of these have been considered as natural variations. Some relatives of *C. acutifolia* Turcz. have been recognized, but the situation was complex, and much has been left to be settled in the future.

A variety, *C. acutifolia* var. *villosula* Rehd. & Wils., was recognized as a near relative. A study of the chromosome number proved it to be a tetraploid form. It is a hardy shrub occupying Zone 5 in central and western China. It grows in thickets in West Hupeh, West Szechuan, and

in the Shensi mountains, the latter bordering on the habitat of *C. acutifolia* Turcz. It may have originated through the doubling of the chromosome number of *C. acutifolia* under circumstances in the past conducive to the disturbance of the chromosome balance. Two specimens labeled *Cotoneaster* sp. grown in the Arnold Arboretum from seed collected by Dr. Rock in the Tao River Basin in western China were triploids.

A large number of species which are considered as belonging to the "acutifolia group" are triploids or aneuploids with approximately the $3n$ number. Included in this category are *C. ambigua* Rehd. & Wils., which the authors considered closely allied to *C. acutifolia* Turcz., and *C. obscura* Rehd. & Wils., which they believed resembled *C. acuminata* which grows in the Himalayas in India. They thought *C. obscura* also resembled *C. foveolata* Rehd. & Wils. of West Hupeh, which seems more probable, although there may have been earlier connections with the *acuminata* ancestors. *Cotoneaster foveolata* Rehd. & Wils. in turn closely resembles *C. moupinensis* Franch., common in the thickets of West Szechuan. These were black-fruited. *Cotoneaster bullata* Bois. and its varieties are red-fruited, and when not in fruit were mistaken for *C. moupinensis*. Further comments show close external resemblance. *Cotoneaster bullata* Bois., according to Wilson, is a relatively rare plant but is widely scattered along the edge of the zone occupied by *C. moupinensis* in West Szechuan.

At first Rehder and Wilson considered *C. tenuipes* Rehd. & Wils. as nearly related to *C. racemiflora* Koch (which is on the other side of the mountains), but they lacked the flowers. Later Rehder placed it near *C. acutifolia* Turcz., which seems more probable, as these forms are all found in West China.

These triploids that resemble *C. acutifolia* Turcz. may have come from the diploid *C. acutifolia* and the tetraploid *C. villosula*. There is also the possibility of intercrossing of *C. villosula* and its descendants with other diploids of the region, as is obvious from the geographical locations and the fact that *C. acutifolia* var. *villosula* is a facultative apomict.

Cotoneaster acutifolia Turcz. may also have contributed some of its characteristics to the flora of the North. *Cotoneaster lucida* Schlecht. was once named *C. acutifolia* Lindl. It is not easily confused with *C. acutifolia* Turcz. It has dark green leaves which are very glossy and lustrous. It has also been found to be a triploid. It grows in the Altai mountains in Mongolia in Zone 4 (Rehder), in thickets at 2000-3000 m., having a limited distribution. This is probably related to *C. acutifolia* Turcz. and may have another relative in *C. melanocarpa* Lodd.

Cotoneaster melanocarpa Lodd. is a tetraploid species which ranges from northern and eastern Europe across Siberia to central and northeast Asia. It is probable that it is another tetraploid form from *C. acutifolia* Turcz. (or even *C. acuminata*, which I doubt) which, having less competition to the north as well as the necessary vigor and better adaptability, has occupied more space than most *Cotoneasters*. It inhabits Zone 4.

Varietal forms of *C. melanocarpa* Lodd. occupy more restricted areas.

The variety *C. melanocarpa* var. *commixta* Schneid. is a 4 n species and *C. melanocarpa* var. *laxiflora* (Lindl.) Schneid. is a 3 n species from central Asia. It may have been a back cross of *C. melanocarpa* with *C. acutifolia* or a cross with *C. acutifolia* var. *villosula*.

Other diploids have contributed variation to the flora around them. *Cotoneaster acuminata* Lindl. is a diploid found in Zone 5 in the Himalayas and on the side away from China. According to Wilson (75) *C. acuminata* Pritzl in Bot. Jahrb. 29: 385. 1900 (pro parte, non Lindley) is under *C. acutifolia* var. *villosula* as a synonym. There are different as to chromosome number and they are geographically separated.

Although they are distinct species, there is some resemblance and a fairly close relationship taxonomically between *C. acutifolia* Turcz. and *C. acuminata*. They may have some common or similar ancestry in the past; at present there are very definite geographical barriers between the species.

Cotoneaster frigida Lindl., a diploid, grows in the Himalayas and is cultivated in Zone 7. Rehder (56) considers *C. affinis* and its variety *C. affinis* var. *bacillaris*, a tetraploid cultivated from Zone 7 (?) to be closely related to *C. frigida*. Bean (3), in his "Trees and Shrubs," remarks that *C. affinis* var. *bacillaris* and *C. frigida* are connected by one or two intermediates. In 1899, W. J. Bean writes in Vol. 55 of The Garden that *C. affinis* is between *C. bacillaris* and *C. frigida*. The tetraploid *C. affinis* var. *bacillaris* may have been formed by a cross between two species, one of which was *C. frigida*, or by the doubling of the chromosome number of *C. frigida*.

Cotoneaster lindleyi, a triploid, also shows affinity for this group, especially *C. racemiflora*. It is an inhabitant of the Himalayas, and is cultivated in Zone 6 (?).

Cotoneaster racemiflora (Desf.) K. Koch is considered by Rehder a very variable species. It is a triploid which ranges in Zone 4 from southern Europe, North Africa, and western Asia to the Himalayas and Turkistan. It has several varieties, var. *desfontaini* (Reg.) Zab. being the typical one, and it is a triploid. It is not found in China, but some of its varieties are found there and are more limited in distribution. *Cotoneaster racemiflora* var. *soongorica* (Reg. & Herd.) Schneid. inhabits West China, Zone 3, and *C. racemiflora* var. *veitchii* central China. These are triploids.

If the species in China are closely related to the species to the west, then a common ancestor must have given rise to those on both sides of the mountains. Its wide range makes *C. racemiflora* look like an older species. It may have come from *C. frigida*, at least as one of the parents, in which there was a doubling of the chromosomes, as is probable in *C. affinis* var. *bacillaris*, or it may have come from a cross of *C. frigida* with *C. acuminata* or an unknown or extinct species. It is apparent that there is a decided difference between the Chinese *racemiflora* species and the typical form.

That the *C. racemiflora* triploids which were grown in close proximity with other *Cotoneasters* breed true shows that apomixis is fairly common.

The seed set is very good. The wide range of these triploid apomicts shows ability to adapt to a variety of locations. *Cotoneaster rosea* shows resemblances to *C. racemiflora*. It may show both *C. acuminata* and *C. frigida* traits. It is a triploid.

Cotoneaster simonsii, first collected in the Khasia Mts. in northern India, shows some resemblance to *C. acuminata* and to *C. rotundifolia*. There is a possibility that in the past it had some common ancestry with the francheti group — to which it is often likened.

Several of the most attractive species of *Cotoneaster* which show various degrees of similarity inhabit West and Central China. They differ from the *acutifolia* group. Among these are *C. francheti*, a tetraploid, and the triploids *C. dielsiana*, *C. dielsiana* var. *elegans*, *C. divaricata*, and *C. nitens*. *Cotoneaster wardii*, a triploid facultative apomict inhabiting Tibet, is very closely related. *Cotoneaster dielsiana* is an apomict. *Cotoneaster zabeli*, which inhabits central China, appears to have some similar traits. It and its variety are both triploids.

The origin of this group is not clear. They are all related to the tetraploid *C. francheti* Bois. The diploid *C. dammeri* grows in central China, *C. conspicua* in W. China. There are also possibilities of having earlier species mixed with ancestors of species from the southern Himalayan groups. *Cotoneaster microphylla* extends into Yunnan. Further study of the *francheti* group is necessary in order to determine its origin.

The *salicifolia*-like group of plants from the Yangtze Basin have been a problem to the systematist. *Cotoneaster salicifolia* Franch., its varieties *floccosa* (Pritz.) Rehd. & Wils. and *rugosa* Rehd. & Wils., *C. rhytidophylla* Rehd. & Wils., *C. glabrata* Rehd. & Wils., and *C. henryana* (Schneid.) Rehd. & Wils., are all evergreen or half evergreen species with prominently veined, elliptic oblong to ovate lanceolate leaves. They have attractive flowers and fruit.

Exell (17) remarks, "I am following the conclusions of Dr. Stapf (Bot. Mag. t. 8999) that *C. henryana* Rehd. & Wils. and the earlier *C. rugosa* Pritz. ex Diels are synonymous." These plants do resemble each other closely, but Rehder & Wilson (56) recognized some differences, and the study of the chromosome numbers indicates that they were correct. *Cotoneaster glabrata* and *C. henryana* are diploid species (Rehder Zone 7 ?). *Cotoneaster salicifolia* comes from Zone 6 (?). Its chromosome numbers have not been determined with certainty. Its variety *C. salicifolia* var. *rugosa* is a triploid from Zone 5.

It may be noted from the zones in which these species are found that they are fairly tender plants. Except *C. rhytidophylla* Rehd. & Wils. they are all growing in the Arnold Arboretum (in fairly protected areas) in Zone 4.

It is not surprising that Thomas (72) remarks, "If these plants are raised from seeds variation results." There are some diploids, *C. glabrata* and *C. henryana*, and some triploids. There may be facultative apomicts in some of this group.

Included by Rehder as a nearly related species is *C. glaucophylla*

Franch. inhabiting West China (Zone 7) which is also a triploid. He calls attention to some resemblance to *C. zabeli*. *Cotoneaster zabeli* is a triploid from central China. A variety, *C. zabeli* var. *miniata* Rehd. & Wils., is a triploid from central China.

The *microphylla* group, mostly prostrate plants, inhabits the Himalayas. E. H. Wilson (75) remarks that it is not seen in China, although it has been reported from Yunnan. These plants are reported to show variation in their seedlings. *C. microphylla* is a diploid. There are several *microphylla* varieties with closely related species, as *C. congesta* Bak. (Himalayas). Rehder mentions *C. conspicua* Marquand, a diploid, as a closely related species. It inhabits West China and Tibet.

It may be noted from the foregoing that the triploids vary more as to range and habitat. Some of them are as limited as the diploids, being reported from only one vicinity. Nineteen out of about forty triploids are reported from West China, four from the Himalayas, and six from Central and West China. Four more are described from Central China, two from North China, and one, *C. multiflora granatensis*, from Spain. All of these show a narrow range.

There are a few more widely ranging triploid species. *Cotoneaster integerrima* Med., an early recognized *Cotoneaster*, is a triploid which is common to Zone 5 in Europe, in the western Himalayas, and in northern Asia to the Altai Mountains in Mongolia. It has been reported from southeast Tibet and Shantung, far from any others that have been reported. Rehder collected it for the Arnold Arboretum in the Savoyan Alps in France, and Anderson collected it in the mountains in Bulgaria. Rehder considers *C. uniflora* Bge., growing in the Altai Mountains, as a closely related species, but comments that it may be only a variety of *C. integerrima*. *Cotoneaster sylvestris* of central China is also mentioned as a closely related species. *Cotoneaster zabeli* of western China shows some characteristics of *C. integerrima*.

Cotoneaster tomentosa (Ait.) Lindl. is somewhat more limited in its distribution. It grows in northern and eastern Europe and western Asia. It has been reported from Kansu. It is considered related to *C. integerrima*, but it is larger and more intense in every detail. It is a vigorous apomictic triploid. *Cotoneaster tomentosa* leaves are more like those of the *affinis* group but heavier and more tomentose; these species differ in fruit and inflorescence.

Another widely distributed triploid, *C. racemiflora*, is found growing from North Africa throughout southern Europe and western Asia to the Himalayas and Turkestan. It is reported at Tomsk in Siberia. J. F. Rock remarks that the typical *C. racemiflora* (Desf.) K. Koch is not found in China, but well-marked varieties are found in Hupeh and Szechuan. The McClaren collectors found *C. racemiflora* var. *veitchii* in the Purple Mountains near Nanking. The variety *C. racemiflora* var. *soongorica* has been collected in West China, Shantung, and Shansi.

Of the large number of triploids only two, *C. glaucophylla* and *C. wardii*, are found in Zone 7 (both questioned); six are in Zone 6, and *C. racemi-*

flora var. *soongorica* is in Zone 3. The remaining triploids in which the chromosome numbers were determined were either varieties or unknown species.

The tetraploids, which are few in number, also vary in the breadth of their distribution. *Cotoneaster acutifolia* var. *villosula* is a tetraploid from central and western China in Zone 4. *Cotoneaster affinis* var. *bacillaris* inhabits Nepal (Zone 7). *C. francheti* western China (Zone 6 ?). *Cotoneaster melanocarpa* ranges in Zone 4 from northern and eastern Europe and the Caucasus to central Asia (having been reported from Tomsk), from Turkestan through Siberia to northeast Asia in Mongolia, Manchuria, Chili and Kansu. The variety *C. melanocarpa* var. *commixta* has a more limited range. *Cotoneaster multiflora* is found in West China. *Cotoneaster melanocarpa* has the widest range of the Cotoneasters except the triploid *C. racemiflora*.

Some of the polyploids show a tendency to adapt themselves over a wider range geographically. The diploids are limited in their range. There is also a slight tendency for the diploids to be more limited zonally, about half being in Zone 7.

All European species so far studied are polyploid. They probably originate from the Himalayan species. No diploids are found in Europe, and all European species show resemblances to those of central and northern Asia. *Cotoneaster multiflora* var. *granatensis* from Spain is supposed to be related to *C. multiflora* from western China. It might, however, be related to *C. racemiflora*, which is not so far apart from *C. multiflora* in distinguishing characteristics. Its leaf pubescence is characteristic of *C. racemiflora*, being one of the characters separating the two species.

When the chromosome number and the tendency to be evergreen were considered at the time of leaf drop there was found to be a slight tendency on the part of the $2n$ species to be more evergreen and therefore more subtropical. There were deciduous diploids, *C. acutifolia* and *C. acuminata*. There were many polyploid evergreens. Some of the plants, both diploid and polyploid, were partially evergreen.

VARIATION AND EVOLUTION

Cotoneaster has long been recognized as a taxonomically difficult genus. Wilson (75) in discussing the similarities of the black-fruited Cotoneasters from China wrote "with *C. acutifolia* Turcz. at one end of the chain and *moupinensis* Franchet at the other, it is almost possible with the material before us to connect the series." As in *Hieracium*, *Crataegus* and *Rubus*, the species and varieties are often separated by minute, but constant differences.

Hybridization is still a prominent factor in the variation and evolution of the Cotoneasters. There is clear evidence of hybridization of the diploid species, both in nature and under cultivation. There is some indica-

tion of crossing between a few of the tetraploids. It is also probable that many, if not most, of the triploids were derived from crosses between diploids and tetraploids. Even some of the apomictic triploids may occasionally hybridize with diploids, as is known to be the case in *Malus*.

Although the great majority of the species of *Cotoneaster* are apomictic triploids, there are some variants among the progeny of some species. Such variation could be caused by occasional sexual reproduction, or it could be the result of internal segregation if the progeny are from unreduced egg cells, as Haskell (34) has suggested for apomictic species of *Rubus*. The meiotic irregularity and loss or non-disjunction of chromosomes could also lead to variant aneuploids, as has been suggested by Stebbins (68). There is some evidence of aneuploidy in a few *Cotoneaster*s, although exact chromosome counts were not possible.

In the triploids the meiotic divisions are irregular, as may be expected, but some species are more irregular than others, with bridges found at anaphase. Although the division process is typical for each species or variety, there is much variation between the species, and due to various degrees of adherence of the homologues, the exact chromosome number is sometimes uncertain. Some of the species may be aneuploid with slight differences in chromosome number; some of the chromosomes may be lacking, but this has not been established.

Perhaps these more irregular triploids are from crosses between distantly related diploids and tetraploids which differ in chromosome structure and result in inversion bridges in the triploid hybrids. The more regular triploids may be autopolyploids between closely related forms. At any rate, the triploids do seem to fall into several rather distinct groups in respect to meiotic behavior.

Polyploidy within the species would also account for some variation since it is known that induced tetraploids are often of a stiffer habit and have larger and more deeply colored flowers than their diploid ancestors. It is just this type of variation that differentiates many of the species and varieties of *Cotoneaster*.

The variation produced by hybridization and polyploidy is "fixed" by apomixis. Although, as Müntzing and others have found, apomixis is not confined to polyploids, it does permit cytologically and genetically heterozygous species to be perpetuated. Slight variations can be maintained in "Clonal Species," a term proposed by Darlington (10).

Apomixis in polyploids permits the constant reproduction of a hybrid which would normally be sterile and would have little survival value. Yet it is known that many artificially produced triploids which must be propagated by grafts or cuttings are superior to either the diploid or tetraploid parent in vigor and in horticultural value (K. Sax unpublished). The fact that most of the species of *Cotoneaster* are apomictic triploids shows that they have high survival values and can be easily propagated.

The polyploid species of *Cotoneaster* do have a wider range of distribution than the diploids. The diploids are largely confined to the Himalayas, West and Central China, while some of the triploids and tetraploids are widely distributed. The triploids *C. racemiflora*, *C. integerrima*, and *C.*

tomentosa have occupied a wide territory. *Cotoneaster lucida*, although limited in distribution, has adapted itself to a colder zone. The tetraploid *C. melanocarpa* has spread over large areas from northern and eastern Europe through Siberia and Manchuria. These widely distributed species are polyploid apomicts.

Excessive uniformity brought about by apomixis might be a handicap, even though under original conditions the triploid or hybrid apomictic species may have definite advantages and greater adaptability. As Stebbins (68) has suggested, the uniformity imposed by apomixis would be a handicap in a changing environment, and the lack of variation would be a block to further evolution.

In *Cotoneaster*, however, there is occasional variation in the progeny of apomictic species. These species still have some plasticity to meet a changing environment, either through occasional sexual progeny, internal segregation, or chromosome irregularity. Thus they have the ability to perpetuate an unbalanced cytological and genetic complex of adaptive value and yet have the capacity to produce variants to meet new environmental conditions.

Polyploidy and hybridization provide most of the variation in *Cotoneaster*. Often the differences are slight, yet they are fixed by apomixis, providing distinct variants which reproduce true to type. Some of these may have a wide distribution. It is this complex of variation due to polyploidy and hybridization, combined with apomixis, that makes the genus *Cotoneaster* a difficult one for the taxonomist. For the horticulturist apomixis is an advantage, since most of the ornamental species and varieties breed true from seed.

SUMMARY

The chromosome numbers were determined in forty-one species and eighteen varieties of *Cotoneaster*. Of these *Cotoneasters* eight taxa were diploid, forty-three triploid, six tetraploid, and two polyploids could not be determined. Some aneuploidy may be present, as several triploids seem to vary.

Progeny from twenty-three species show that two diploids reproduced sexually. The rest reproduced apomictically, an occasional variant appearing among three of the nineteen triploids: *C. nitens*, *C. simonsii*, and *C. wardii*. One tetraploid was a facultative apomict.

The diploids are limited in their geographical distribution, as are most of the triploids and tetraploids. Among the triploids three species, *C. integerrima*, *C. racemiflora*, and *C. tomentosa*, show wide distribution. One tetraploid, *C. melanocarpa*, is found over wide areas. The diploids showed a slight tendency toward zonal, as well as geographical limitation.

Apomixis stabilizes a species, but the genus *Cotoneaster* is given flexibility through sexual reproduction and through facultative apomixis. There are probably some obligate apomicts, i.e., *C. dielsiana*.

Apomixis and polyploidy are responsible for the taxonomic complexity of the genus *Cotoneaster*.

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THE DIRECTOR'S REPORT ON THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1954

The fiscal year of 1953-54 was a momentous one for the Arnold Arboretum, marking as it did the solution of long-standing problems of space, housing and care of collections which have for over a decade hindered the work of the Arnold Arboretum.

On January 19, 1953, the President and Fellows of Harvard College (the trustee of the Arnold Arboretum), in a detailed and careful vote, stated that "In the exercise of its duties as trustee of the endowment funds held in trust for the purposes of the Arnold Arboretum, the Corporation determines that it is in the best interests of the Arboretum and will promote the purposes of its endowment to remove to a central building in Cambridge the main body of the library and herbarium of the Arboretum related to research, and to retain in Jamaica Plain such books and specimens as may be required to provide there a working library and herbarium." This proposal had long been advocated as a solution to the problems of the Arboretum which previous directors have stated in their annual reports. (See Annual Reports 1936, 1938, 1940, 1941, 1942 and following.) The Administration Building in the Arboretum had become overcrowded. Floor space was no longer available for the addition of steel cases, and as temporary expedients, display cases and cardboard herbarium boxes were used to store approximately 20% of the mounted herbarium and all of the material awaiting determination and mounting. The library was equally crowded to the point where it was becoming difficult to care for the valuable books properly. This latter condition had been alleviated by transferring, for use and storage, many of the Arboretum books to the Harvard Forest and to Cambridge. However, even with these measures, additional shelf space could not be found in the Administration Building. Working space for staff members had become restricted by the growth of the collections and the library. To solve these and other problems, the Corporation vote was welcomed by a majority of the staff of the Arboretum.

The vote of the Harvard Corporation called for the appointment of an Arnold Professor, a post unoccupied since the retirement in 1946 of Dr. E. D. Merrill. In October the Corporation, with the approval of the Board of Overseers, appointed Richard Alden Howard as Arnold Professor and Director of the Arboretum. Dr. Howard was also appointed Professor of Dendrology within Harvard College. All appointments were effective February 1, 1954.

The Harvard Corporation had voted that a portion of the herbarium and library was to be moved to a new building in Cambridge known as the Harvard University Herbarium Building. One million dollars was assigned from unrestricted funds of the University for the construction and equipping of this building. The Arboretum collections and library would thereby receive adequate housing and the staff working equipment at no

capital cost to the Arnold Arboretum endowment. Construction of the building was completed in February 1954.

The Arnold Professor, by vote of the Corporation, was to implement the move. Serious consideration was then given by the director and the staff of the Arboretum to the selection of books and herbarium specimens to be retained in Jamaica Plain. When tentative plans were formulated, Dr. Howard, in accordance with the vote of the Corporation, consulted with Dr. William J. Robbins, Director of the New York Botanical Garden, regarding what specimens were to be left in Jamaica Plain as a working herbarium. He also consulted with Dr. Keyes Metcalf, Director of the Harvard University Libraries, regarding what books were to be retained in Jamaica Plain. Each of these conferences produced a final plan which determined the nature of the Arboretum's collections of specimens and books in each of the two locations. Dr. Robbins and Dr. Howard determined that the vote of the Harvard Corporation could be best implemented by establishing in Jamaica Plain a working herbarium devoted to the study and advancement of knowledge of horticultural plants. To that end they made seven recommendations as follows:

1. That all cultivated specimens in the herbarium of the Arnold Arboretum representing taxa now under cultivation in the Arboretum and elsewhere be retained in Jamaica Plain.
2. That sufficient additional specimens of taxa related to a given cultivated group be retained to insure working control of that group.
3. That spontaneous or native specimens be used to supplement poorly represented cultivated taxa.
4. That representative specimens of all taxa of certain major cultivated groups be retained. For example, it is proposed to have in Jamaica Plain all material of the difficult genus *Crataegus*, and to have representatives of all taxa of the Conifers, *Rosa*, *Rhododendron*, *Cotoneaster*, *Quercus*, *Syringa*, *Viburnum*, *Lonicera*, *Fraxinus* and *Ulmus*.
5. That additional specimens be returned to the herbarium at Jamaica Plain as their need becomes known; i.e., new introductions, new cultigens, or additional material found necessary for determination.
6. That this herbarium be maintained as an active herbarium and that additional cultivated material, e.g. herbaceous specimens, be added in future years to make the herbarium at Jamaica Plain a complete working herbarium for determination and study of all groups of cultivated plants.
7. That all type specimens of cultivated taxa remain in the Jamaica Plain herbarium and be clearly marked and properly housed.

The specimens to be retained in Jamaica Plain number approximately 100,000 specimens and are housed in 96 steel herbarium cases, creating in itself one of the outstanding horticultural herbaria of the world.

A similar set of proposals was worked out by Dr. Metcalf and Dr. Howard regarding the library books to be retained in Jamaica Plain. Again, in accordance with the vote of the Harvard Corporation and for the best interests of the Arboretum, Dr. Metcalf and Professor Howard

recommended the establishment of a working library devoted to the study and advancement of knowledge of horticultural plants. To that end they recommended to the Corporation the following proposals:

1. That the library in Jamaica Plain retain a complete set of all publications of the Arnold Arboretum; i.e., the serial publications *Arnoldia*, the *Journal of the Arnold Arboretum* and *Sargentia*, as well as the complete sets of publications by staff members. All Sargent, Wilson and Rehder publications will be kept in Jamaica Plain.
2. That reference books for horticultural study and research are to be retained. These will include basic textbooks, floras, garden dictionaries, horticultural encyclopedias, and all books which normally fall in the library classification of horticulture, botanic gardens, etc.
3. That a selection of books on dendrology, ecology, physiology, pathology, economic botany, entomology, biography and natural history, as well as books on color will remain in Jamaica Plain.
4. To coordinate the interests of the herbarium with those of the library, there will be in Jamaica Plain all books dealing with roses, rhododendrons, lilacs, and similar groups, as well as monographs of *Crataegus*, *Quercus*, and the Conifers, and other horticultural books and monographs which will strengthen the value of the horticultural herbarium.
5. Additional periodicals of particular value to horticultural research and reference, such as Curtis's Botanical Magazine, Horticulture, Gartenschönheit, La Belgique Horticole, Revue Horticole, Gardener's Chronicle, Journal Royal Horticultural Society, etc., will be retained.
6. Folio volumes useful to horticulture are to be left in Jamaica Plain.
7. The large collection of Wilson photographs, photos of botanical gardens, cultivated plants, etc., are to be considered library material and retained in Jamaica Plain. The Rehder card catalogue considered essential in the use of the cultivated plants in the herbarium also will remain in Jamaica Plain.
8. All books, manuscripts and comparable reference material are to be catalogued on cards available in Jamaica Plain, and suitable designation of the location of these books is to be made in the Union Catalogue at Widener Library.
9. Additional books or similar reference material that may be found necessary in Jamaica Plain will be returned for permanent deposit in the library of the Administration Building.
10. The library of the Arnold Arboretum in Jamaica Plain and in Cambridge is to be considered in the future, as it is now, a reference and non-circulating library.

These proposals for a library dealing with cultivated plants consider approximately 7000 volumes of the total Arboretum library, including 1800 periodicals and 100 folio volumes.

Further consideration was taken by the staff as to the proper housing and location of books and specimens in the Administration Building in Jamaica Plain. Tentative plans were drawn for a redesigning of the interior of the Administration Building for horticultural activities. It was

proposed to house the library, offices, and herbarium on the first floor of the building. With the additional space available, a lecture-demonstration room will be possible, also on the first floor. Adequate storage and expansion for both the library and herbarium and sufficient working space for the staff is again possible in the building.

After all aspects of the proposals and plans were reviewed by the staff of the Arboretum, Dr. Howard submitted a report to the Corporation stating his recommendations for the implementation of the Corporation vote of January 19, 1953. The Corporation at their meeting on May 17, 1954, invited Dr. Howard to appear and to describe the procedures followed in preparing his recommendations. Later in the same meeting, the Corporation voted that the several recommendations presented by the Arnold Professor and Director of the Arnold Arboretum were in accordance with the statement of policy in the resolution of the Corporation of January 19th. The Corporation accepted Dr. Howard's recommendations and authorized him to proceed in accordance with those recommendations to carry out plans for the removal from the Administration Building in Jamaica Plain the herbarium specimens and books selected for location in the University Herbarium in Cambridge.

With this authorization the move began on June 7th and was in progress at the end of the fiscal year. The herbarium staff proceeded to draw out the herbarium specimens to be retained in the cultivated herbarium and to arrange these in the steel cases on the first floor of the Administration Building. The librarian, with additional assistance, selected the books to be retained in Jamaica Plain and these were arranged temporarily in the library reading room on the second floor until their permanent quarters on the first floor have been completed. The shifting of both the herbarium and the library was coordinated in such a way that there was no interruption of horticultural work or of service determinations. By July 1st the herbarium of cultivated plants in the Administration Building was completely organized and in use. Casey and Hayes Company, movers, were charged with the task of moving the herbarium cases with the specimens intact to the new building. The library to be moved was so organized that the books were taken from shelves in Jamaica Plain and placed on previously designated shelves in the new library in such a fashion that the books were always in order. Only the highest praise can be suggested for care afforded both the books and the specimens in the course of the move. The Art Metal Company, which originally supplied the steel herbarium cases of the Arnold Arboretum, was responsible for disassembling the cases in Jamaica Plain and reassembling them in Cambridge. That work is in progress. All cases are to be checked and new felts applied where necessary to assure that the old cases in their new location will be bug-proof. A large number of herbarium specimens had to be transported from Jamaica Plain to Cambridge in the cardboard herbarium boxes which had been their location for a decade. Eventually these specimens will be arranged in proper sequence in the regular herbarium and all will be stored in steel cases. The appropriation by the Corporation from University

funds allowed the purchase of 430 additional steel herbarium cases. The majority of these will be used to house the Arboretum's collections. Within the next year the Arboretum specimens for the first time in many years will all be housed properly in steel cases.

The Director can only speak with praise of the yeoman's service rendered by the Curator, the Librarian and many members of the staff who worked so hard to implement this move. A major goal in the care of the Arboretum's collections is near attainment, and while many months of hard work remain, the best interests of the Arnold Arboretum have been fully considered in the activities of the past year involving the move.

Horticulture:

Living collections of plants such as those that comprise the Arboretum's collection require constant care. The excellent condition of the grounds throughout the year and the outstanding floral display of the spring of 1954 are indicative of the activities of the horticultural staff.

During the past year approximately 150 species and varieties of new plants were added to the collections in Jamaica Plain. Many others were received either as seeds or living plants. These have been grown or propagated and are now being tested in our nurseries. A total of 152 shipments including 790 species and varieties was received. Most of these came from arboreta, gardens and nurseries in the United States and Japan, but shipments originated also in eight other countries. Over 50 species and varieties of Post Entry Quarantine plants were released by the U.S. Department of Agriculture, Bureau of Plant Quarantine, and these are being propagated for distribution as they show ornamental value. The propagation department prepared 7396 plants for our collections or for exchange or other distribution. These plants were propagated: cuttings, 4164; grafts, 2717; seeds, 485, and layering, 30. During the past year 144 shipments of plant materials were sent to cooperating institutions in eleven countries. Five small tree species, either new or extremely rare in America, were propagated and distributed to 24 cooperating nurseries which requested materials from a previously circulated list. Nearly 1000 individual plants were distributed to "Friends of the Arboretum" throughout the year. Several large yews and other shrubs were given to the Department of Buildings and Grounds of Harvard University for planting about the University Herbarium Building and other college buildings.

Pruning, fertilizing, spraying and planting operations continue throughout most of the year at the Arboretum. In the past year the base of Hemlock Hill was cleaned of weed growth, opening an area for a new hemlock planting at some future date. Many weed plants were pulled from the azalea bank on South Street and in the Kalmia collection on Hemlock Hill. The *Taxus* collection and the large pines along Walter Street were given a much-needed thinning, as were the azaleas on Bussey Hill.

Thirty-one cords of manure were spread on collections needing fertilizer.

These collections included the plantings of *Carpinus*, *Juniperus*, *Chamaecyparis*, *Viburnum*, *Rhododendron* and some of the *Rhododendron obtusum kaempferi* in the woods near the ponds. The *Rhododendron* collection had a splendid display of bloom this year as a result of repeated fertilizer applications of past years. Castor pumice has been used extensively on these plantings. Summer watering has also improved the condition of these plants.

The bank along the railroad tracks was sown to grass in the fall and several groups of conspicuous blooming trees were planted there this spring. Within a few years we hope to develop this bank into a colorful display, primarily for the benefit of the commuters on the Dedham branch of the New York, New Haven and Hartford Railroad.

A new "Bean" 400-gallon hydraulic sprayer was purchased to be drawn by tractor. It has become increasingly evident that control of all insects and diseases in the Arboretum merely by mist spraying is impossible. Both mist and hydraulic spraying are used now with better coverage and control that was formerly possible. Spray equipment was used on 24 different days last year. Particular attention to sprays and techniques of spraying for use in arboreta and parks is being given under the direction of the Superintendent and his staff. Fireblight, which in the past few years has become a serious threat to the large crab apple collection, was apparently held in check this year by the experimental use of "Agrimycin," one of the new antibiotics. A supply of this material for testing was donated by the Chas. Pfizer Company of New York. Weed control by the use of chemicals on a rigid spraying schedule has made poison ivy much less evident this year than before. The plant still grows in the Arboretum, however.

The locations of all cultivated plants on the 265 acres of the Arboretum are recorded on 74 standard maps scaled at 20 feet to the inch and 34 additional enlargements covering the congested areas. Of these 108 maps, approximately one-third are carefully field-checked each year. The condition of the plant is noted so that it can be propagated, fertilized, sprayed, labeled or given any treatment deemed necessary. Each year it is necessary to replace from 1500 to 2000 display labels which have disappeared or are illegible. At the same time identifications are checked and kept up to date with current taxonomic revisions. Last spring all the lilac collection was checked during the flowering period. A few plants were discarded as not being true to color and the remainder are now considered correct according to the most recent survey of "Lilacs for America," published by the Lilac Survey Committee of the American Association of Botanical Gardens and Arboretums. To further enhance the value of this collection to the public, selected plants were labeled "best of the variety" during the flowering season.

The collection of photographs owned by the Arboretum is used constantly for reference by the staff. Prints of these photographs are used by the staff to illustrate articles for publication. Photographs from our

files were also used in several national garden magazines and in newspapers. In recent years a collection of 35 mm. Kodachrome slides and 5×7 Ektachromes has been built up. These are used to illustrate lectures and publications. This collection is increased yearly and its use grows. Many of the photographs in these collections are made in private gardens in the vicinity of Greater Boston. The splendid cooperation of home owners who have unusual or interesting plant materials being used to advantage and who have given Arboretum staff members permission to photograph them is greatly appreciated. Within the past year post-cards have been made from some of the kodachromes taken in the Arboretum. These are on sale at the Administration Building and in Boston and have proven popular among visitors.

The staff of the Arboretum remains active in the field of plant propagation. The use and effect of various plastic films in vegetative propagation is receiving considerable attention. Species of *Magnolia*, *Ilex* and *Acer* which are normally difficult to root are being tried under polyethylene plastic. The effect of polyethylene plastic as a tie material over graft unions is being tested on species of *Picea*, *Pinus* and *Abies*. A polyethylene grafting case has been used in propagation of species of *Ulmus*, *Quercus* and *Betula*. The same plastic film is being tested as a means of preventing the drying of seeds during stratification.

Acer griseum, one of the unusual maples in the Arboretum collection, is being tested for the effect of different root stocks on compatibility. Various concentrations of hormones on the rooting of *Rhododendron* species and varieties is being undertaken. Artificial pretreatment of seeds requiring a high temperature period followed by a low temperature is being applied to species of *Viburnum*, *Cotoneaster* and *Acer*. Reports will be published on the results of these experimental projects as the work progresses.

The horticultural staff has also demonstrated the popularity of the Arboretum collections through a program of adult education. Informal classes were held in the greenhouses, and the Fall and Spring Field Classes conducted by Dr. Wyman have attracted a record attendance in the past year. Conducted tours of the grounds are available to large groups requesting such service in advance. Many garden clubs took advantage of this service during the past year. The Massachusetts Horticultural Society had its regular field day at the Arboretum on May 15th, and four busloads of visitors attending the National Convention of the American Society of Landscape Architects were conducted through the grounds by members of the staff.

The ground cover and small tree display plots at the Case Estates in Weston are proving to be of increasing interest to visitors. Classes from four different colleges in New England made trips to Weston to study these collections. An experiment in the use of maleic hydracide and Crag herbicide is under way at the Case Estates. Preliminary results indicate that these materials may be valuable in reducing the hand labor required in the Arboretum as well.

Cytogenetics:

A number of new hybrid ornamental apples produced at the Arnold Arboretum have proved to be outstanding and are being propagated for distribution. The hybrids with *Malus Sargentii* are of special interest because of their dwarf habit and brilliant foliage during the spring and early summer. The hybrids, like the *M. Sargentii* parent, are facultatively apomictic and tend to breed true from seed.

Species hybridization is common in the subfamily *Prunoideae* (Rosaceae), and a number of spontaneous hybrids between *Prunus Besseyi* and other species have been found. An excellent example of the stability of the genus is shown in the artificial cross between *P. Besseyi* of central North America and *P. tomentosa* from eastern Asia. Although these species differ in many characters and have been separated for hundreds of thousands of years, they cross readily and the F1 hybrid is fertile.

The "Merrill" Magnolia, a hybrid produced fifteen years ago, has proved to be vigorous and early-flowering. It became available to the horticultural public from commercial sources in the spring of 1954.

Dwarfing rootstocks and bark inversion are being used for the development of dwarf ornamental trees. The bark inversion technique is being used to induce early flowering in ornamental trees and vines which are reluctant to produce flowers.

Hally J. Sax (Mrs. Karl Sax), utilizing the extensive living and herbarium collections of the Arboretum, completed a cytotaxonomic study of the genus *Cotoneaster*. Most of the species were found to be apomictic triploids. There is some evidence of facultative apomixis in these triploid species. Thus the species is able to perpetuate hybrid complexes through apomixis, yet retain some genetic plasticity to meet new environmental conditions by occasional hybridization.

Dexter Sampson, a graduate student, continued his work on the cytological analysis of the progeny from triploid hybrids in *Philadelphus* and *Forsythia*. Bradford Johnson, another graduate student, began a study of the cytology of facultative apomixis in *Malus*.

Comparative Morphology:

Professor Bailey has completed his task of preparing material for publication in book form by the Chronica Botanica Company. This volume which deals with salient trends of anatomical research during the period 1909-1953 will be released for sale in the near future. Miss Margery P. F. Marsden has completed her intensive investigation of *Clerodendron trichotomum* Thunb. and received the doctorate from Radcliffe College in June. Mr. Chi Ling Chen developed symptoms of tuberculosis early in the fall and is having to spend at least a year at the State Sanatorium in Rutland. This was extremely unfortunate, not only in postponing completion of his work on the Sapotaceae for the doctorate, but also in depriving Professor Bailey of his expert assistance in preparing the wood collection for transfer to its quarters in the new botanical building.

The wood collection was initiated by Professor Sargent during the early years of his administration of the Arnold Arboretum. It has subsequently been enlarged and strengthened by additional accessions at the Arnold Arboretum and by successive contributions made by the Forestry School, the Bussey Institute and the Department of Biology. Since 1936, it has been housed, as have staff members of the Arnold Arboretum concerned in its use, in the Biological Laboratories without cost to the Arboretum. For a number of years the Department of Biology provided financial assistance in the making of catalogues and microscopic slides. Furthermore, Professor Wetmore and his associates contributed much time and effort to expanding and improving the collection. In transferring the much enlarged collection, new steel cases and many new trays have been provided by the University. The Biological Laboratories also generously contributed a large number of the trays in which the collection was formerly stored. In its new quarters, the collection is housed in close proximity to the collections of fruits and seeds and slides of pollen, leaves and flowers. Thus, any taxonomist working with herbarium specimens now has efficient and convenient access to supplementary data contained in these extensive and very valuable collections.

The Herbarium:

The activities of the herbarium staff during the past year were involved in the preparations to implement the vote of the Harvard Corporation. The Curator, Dr. Kobuski, and Miss Perry devoted regular time and many extra hours to the designation and separation of the horticultural herbarium and the preparation of the non-horticultural material for the move. In spite of these steps of preparation, the regular activities continued in the herbarium. During the past year 3560 specimens were mounted and added to the herbarium, which now contains 675,119 sheets. A total of 12,421 specimens were sent out in exchange, 11,121 to foreign institutions and the remainder to American herbaria. New collections received at the Arboretum number 27,758 specimens. Of these, 12,000 specimens came as gifts or in exchange, while approximately 16,000 specimens were received from expeditions or collectors sponsored completely or in part by the Arnold Arboretum. Nearly 85% of the incoming materials were received from Malaysia and Asia, forming a significant addition to the valuable collections already in the Arboretum from this area. Among the noteworthy accessions are 14,000 specimens collected by L. J. Brass on his most recent trip to New Guinea; Richard Schultes' collection of 3,500 specimens from the Amazon; 2,000 specimens from the Philippine Bureau of Science collected in oriental Mindoro, and 3,500 specimens from Japan, the Ryukyu Islands and other accessible areas of Asia. An active exchange continues between the Bogor Herbarium in Java and the Arnold Arboretum. During the past year the Arboretum received 2,400 specimens from the Bogor Herbarium collected in various regions of Indonesia.

The number of requests for loans of specimens from the Arboretum

collections continues high. A total of 5,457 specimens were sent out on loan during the year to twenty-two different institutions. Foreign requests for loans numbered eleven.

During the year, staff members conducted research on plant families and areas of their specialties. Dr. Howard was appointed Senior Botanist on a project sponsored by the Institute of Jamaica in Kingston, Jamaica, British West Indies, to survey the native vegetation on bauxite soils on that island. The project hopes in the course of this work, to determine what plants of potential economic value can be grown on mined-out bauxite areas. Dr. Howard continued his work on the vegetation of the Caribbean Islands and made some progress on monographic studies of the genus *Coccoloba*.

Dr. Kobuski continued his work on the Asiatic members of the *Theaceae* and specifically towards a treatment of this family for the Flora Malesiana. He also identified several large collections of this family for various herbaria.

Dr. Johnston concentrated on his studies of the *Boraginaceae*, with a special interest in the herbaceous genera found in Asia and the Middle East.

Dr. Perry continued her work on the New Guinea flora, giving special attention to the recently received collections of L. J. Brass.

Dr. Hu is completing a monographic study of the ornamental genus *Philadelphus* and supervises the initial stages of the preparation of a list of the species of flowering plants reported from China.

Dr. Merrill is now receiving the proofs on his book regarding the botany of Captain Cook's two voyages in the Pacific. It is expected that this major contribution will be published in the fall.

The Library:

The preparation and implementing of plans to organize a horticultural library and the separation of those books to be moved to Cambridge formed a major portion of the work of the librarian and the library staff during the past year. The Corporation requested in its vote that all Arboretum books to be housed in Cambridge be distinctly marked. Thus, within the past year all books which are part of the Arboretum library have been checked and marked where need be, with a stamp or sticker on the back, an embossed imprint within the pages, or a bookplate, or a combination of these. An excellent selection of books of horticultural use was made with the cooperation of Dr. Wyman and other members of the staff. These books to remain in Jamaica Plain will eventually be located in a newly designed library and reading room on the first floor of the Administration Building, with room for expansion or for little used volumes on the second floor of the herbarium wing.

Additions to the library by gift, purchase or binding totaled 271 volumes. The library now contains 48,673 bound volumes on the shelves. Pamphlets numbering 206 were added to the pamphlet collection, bringing that collection to a total of 15,410 items. Five hundred and four

catalogue cards were added to the main catalogue and 1206 cards were added to the Gray Herbarium index of American species. Inter-library loans showed an increase over past years, although many additional requests were answered by typing short descriptions, or through the use of microfilm and photostat copies.

Exhibits and Displays:

The Larz Anderson Collection of Japanese Dwarf Trees was featured at the exhibit of the Arnold Arboretum at the Spring Flower Show of the Massachusetts Horticultural Society. The plants were exhibited in a setting of a Japanese garden. An interesting bamboo shelter was erected to shelter these plants in a fashion comparable to that used in Japan. Three excellent Kurume azaleas loaned by Mr. John Ames added color to the display. A first prize and a gold medal were won by this display.

Several additional displays of living plant materials were furnished for other shows of the Massachusetts Horticultural Society during the year. An Arboretum display of sprays of flowers, tree photographs and Ektachrome display panels occupied a featured location at the National Convention of the American Society of Landscape Architects at the Hotel Somerset. This exhibit attracted much attention and was mentioned in the programs and news releases of the meetings.

Publications:

Four issues of Volumes 34 and 35 of the Journal of the Arnold Arboretum were issued quarterly totaling 522 pages. Dr. Kobuski serves as editor of the Journal, assisted by an editorial board of other members of the Arboretum staff. Twelve numbers of *Arnoldia* were issued under the editorship of Dr. Wyman and were distributed to the Friends of the Arnold Arboretum and additional subscribers so that the total distribution now numbers 2,200. The subscription price of *Arnoldia* was raised to two dollars per year. This represented the first increase in price since this publication first appeared. A demand for back numbers of *Arnoldia* increased to the point where it seemed desirable to accept an offer of the D. Van Nostrand Company of New York to publish some of these as "The Arnold Arboretum Garden Book." Some forty-five issues were selected and Dr. Wyman wrote an introduction and foreword for this book. Proof of the book is now being received and publication is expected in the fall of 1954.

Gifts and Grants:

The Arboretum is fortunate to receive a large number of gifts from individuals interested in the work of the organization and the staff. Most of these are received as "memberships" in the "Friends of the Arnold Arboretum." During the past year 431 memberships were received. Such gifts are assigned, unless otherwise designated, to a fund called "gifts for cultural purposes" and are used exclusively to sponsor additional work

on the grounds, such as developing new collections, additional care for the plantings or for research and work leading to the development of new hybrids, dwarf plants and similar projects. Additional gifts were received designated for specific purposes. One gift from a Friend of the Arboretum was to be used to support foreign collectors and thereby obtain for the Arboretum additional material of horticultural value. It is hoped that this meritorious fund can be increased in future years. Another large gift was placed at the discretion and joint use of Dr. Reed Rollins, Director of the Gray Herbarium and Dr. Howard, Director of the Arboretum, to be used for research in systematic botany for the benefit of both the Arnold Arboretum and the Gray Herbarium.

The Arboretum received a bequest from the estate of Emery Holden Greenough which was assigned to the endowment of the Arboretum. Through the generosity of Mrs. Martha Peters, her home and the land thereabout on South Street was given to the Arboretum. It is hoped that eventually when funds are available the setting of this old house can be used as a demonstration landscape area to show plants for small homes in a good setting. The adjacent land when reconditioned will be of great value to the Arboretum as a nursery area.

Numerous Friends have given books on plants and flowers to the Arboretum. The value of these books is determined by the librarian and reported to the donor for income tax purposes. Many of the books are welcome additions to the library, while others serve as replacements for worn books long in use.

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